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PART I: BOTANY AND FORESTRY

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PART I: BOTANY AND FORESTRY

PART II: ZOOLOGY

PART III: GEOGRAPHY AND GEOLOGY

PART IV: GENERAL SECTION

ANTHROPOLOGY, ECONOMICS, FINE ARTS,
FOLKLORE, HISTORY AND POLITICAL SCIENCE,
LANGUAGE AND LITERATURE, PHILOSOPHY,
PSYCHOLOGY

PAPERS OF THE
MICHIGAN ACADEMY OF SCIENCE
ARTS AND LETTERS

EDITORS

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VOLUME XXXVII (1951)

PART I: BOTANY AND FORESTRY

"Pusilla res mundus est nisi in illo
quod quaerat omnis mundus habeat."

—SENECA, *Naturales Quaestiones*

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BOTANY

SOME OBSERVATIONS ON THE ANATOMY OF THE COMMON GERANIUM

CHESTER A. ARNOLD

ALTHOUGH the common geranium, *Pelargonium zonale* (L.) Ait., is widely used in elementary botanical teaching, the available information on the anatomy of this plant is scant. The structure of the leaves and roots, especially in relation to their physiological activities, has received some attention, but a search through the literature on plant anatomy reveals only casual references to the stem. Even these are not numerous. MacDuffie (3) and Thompson (5) give some information on the form and structure of the vessels, and Heimsch (2) refers to several anatomical features of the secondary xylem that possess taxonomic significance. Hegedüs (1) mentions the fact that independent bundles become connected by interfascicular cambium in the young stem. Metcalfe and Chalk (4) summarize the literature relating to the Geraniaceae that has appeared since the publication of Solereder's *Systematic Anatomy of Dicotyledons* in 1908.

The observations recorded in this paper were made from a set of fifty slides prepared by Triarch Botanical Products. All the sections were taken from the basal part of a potted plant about a foot high, and each slide bears a transverse and a radial-longitudinal section. Although the exact age of the plant is not known, the degree of development of the tissues indicates that in all probability it was at least a year old. The stain used was Conant's quadruple stain. Because the sections were prepared with classroom use in mind, they were cut thicker than they would have been for research purposes. If one were to undertake a thorough analysis of the geranium axis, the sections not only should be thinner, but should also be taken at several places between the apex and the base, and special stains should be applied to bring out particular features. However, regardless of the fact that the sections at hand were not prepared primarily for research, they show quite adequately details of the xylem structure, especially if supplemented with mounts of macerated tissue.

GROSS ANATOMY

The primary vascular system of *Pelargonium zonale* is a dictyostele, but an interfascicular cambium forms close to the growing point, and sections cut only a few millimeters below the apex show a complete cylinder. In all sections showing secondary growth the positions of the vascular bundles are indicated by blunt wedges of primary xylem that project slightly into the pith. Hegedüs says that the complete set of bundles is not formed by the procambium, but that some are produced by the interfascicular cambium. Between the primary xylem masses the secondary xylem comes in contact with the pith. The relation between primary and secondary tissues is shown in Plate I, Figure 1.

In the sections examined the secondary xylem is a compact layer of tissue about three quarters of a millimeter wide. The absence of well-developed rays is a conspicuous feature. The secondary phloem, which consists entirely of thin-walled cells, is one third to one half as broad as the xylem. This is succeeded by the so-called "pericycle" of the textbooks, a band of thick-walled fibers two or three cells wide. This band is interrupted at several places and parenchyma fills the breaks. A study of the origin of this layer would probably show that it is primary phloem, as has been found to be the case in *Linum* and a few other plants. The designation "pericycle" is therefore appropriate for this tissue only if it is used to distinguish it from the remainder of the phloem. There is no visible endodermis. The cortex is fairly uniform and is made up of rounded or oval cells with numerous intercellular spaces. It is about as thick as the xylem. At the stage studied there is a periderm layer, slightly thinner than the cortex, completely enveloping the stem. It is still covered with the stretched epidermis. At several places around the periphery of the section the periderm layer has split owing to increase in the diameter of the stem (Pl. I, Fig. 1 at left). Although these breaks probably perform the same function as lenticels, they lack the structure of lenticels.

DETAILED ANATOMY

Pith.—The pith, which occupies fully half of the diameter of the stem at the place where the study was made, is a relatively uniform tissue of thin-walled cells.

In cross section the pith cells are rounded and slightly faceted

because of mutual contact. Adjoining each cell are four to six triangular intercellular spaces. In longitudinal section the cells appear more nearly square and are arranged in fairly well organized vertical files. Their thin walls bear rather numerous simple pits that vary somewhat in size and shape. The only variation in cell structure within the pith is the occurrence here and there of groups of very small cells containing crystals of calcium carbonate between the ordinary cells of a file. The size of these cells and the position of the groups indicate that they originate by division of a single ordinary cell. The pith cells continue without marked diminution in size right up to the wood, although those in the outermost layer may be narrower and longer than the others. There is no medullary sheath.

Primary xylem.—The broadly triangular primary xylem masses are composed of irregularly arranged cells that contrast rather sharply with the orderly arrangement of the cells of the secondary wood. The one or two annular tracheids that make up the protoxylem are slightly immersed in the small-celled parenchyma that constitutes the point of the wedge. The innermost metaxylem consists of a few small tracheids with loosely wound spiral wall thickenings. These are larger than the protoxylem elements but smaller than those metaxylem cells that follow. The bulk of the metaxylem is composed of vessels and tracheids that are about as wide as the vessels in the secondary wood. These contain both annular and spiral thickenings, both types frequently being present in the same element. The rings are so close together that they simulate the scalariform condition, and in microtome sections it is difficult to ascertain with certainty which kind of sculpturing is present. The situation is plainly revealed, however, in macerated tissue.

Usually these spiral and annular-spiral elements extend all the way to the secondary wood, thus making up the bulk of the metaxylem. Sometimes scalariform and reticulate types intervene, but they are never abundant. The scalariform type is rare, apparently existing only where the elements are too narrow to accommodate the other form of thickening.

Secondary xylem.—The secondary xylem of *Pelargonium zonale* is a compact tissue of fibers, vessels, and parenchyma. Rays of the kind present in most secondary wood are absent. Occasionally, however, radially aligned rows of parenchyma cells extending from the

pith to the cambium constitute obscure rays, but they are never numerous. The vertical extent of these structures has not been determined. According to Heimsch (2), rays in the Geraniaceae are characteristically obscure. Wood fibers of a special kind, for which the designation "nucleate fibers" is proposed, make up the bulk of the secondary xylem (Fig. 1 *a-h*). The necessity of coining a special term for them is explained in the concluding part of this paper.

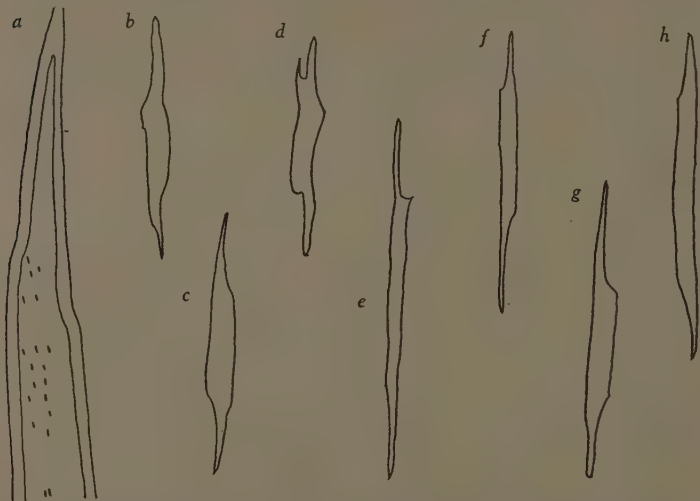


FIG. 1. *a*, terminal portion of nuclear fiber, greatly enlarged, to show distribution of the minute pits, $\times 450$; *b-h*, camera lucida sketches from mounts of macerated xylem, to show variations in size and shape of nucleate fibers. $\times 80$

The nucleate fibers are fiber-like cells with moderately thickened lignified walls and protoplasmic contents (Pl. II, Figs. 1-4), and small but conspicuous spindle-shaped nuclei. These nuclei measure about 3 by 23 microns (Pl. II, Figs. 2, 4). The walls contain very small vertically elongated pits that are about 2 microns wide (Fig. 1*a*). They appear to be simple. They are scattered over the walls, and the number on a single radial facet commonly ranges from 12 to 20, although the variation is great. They may be clustered into irregular groups of two to five or more, or they may form a multiple band along the median portion of the facet.

In appearance a nucleate fiber resembles an ordinary short wood fiber. Its oblong body portion is about as long as the cambial initial from which it was derived, but the tips became attenuated during development, so that the overall length is considerably greater. The majority of the nucleate fibers range between 240 and 750 microns in length, with approximately 50 per cent between 300 and 500 microns. The radial dimensions range between 28 and 38 microns at the widest place, and the tangential diameters are slightly less. In a specimen of average length the tapering end portions make up about half of the total length of the cell. Occasionally the tips are forked (Fig. 1*d*). Starch is frequently present, especially in those nucleate fibers near the pith.

The vessels, as seen in transverse section, are grouped into rather well organized radial rows, forming the so-called "pore chains" of wood technology (Pl. I, Figs. 1, 3). Because of the thin xylem layer in the material examined, some of the chains extend most of the way across it. Most of them, however, are short, consisting of two to four elements. Solitary vessels also occur.

In all sections, but particularly in the transverse one, the vessels stand out conspicuously because of the marked difference in size between them and the other cells. The area of the cross section of a single vessel is roughly four times that of a nucleate fiber or xylem-parenchyma cell, but, as in these cells, the radial dimension is slightly greater than the tangential one. All the walls have about the same thickness.

A vessel element is about as long as the broad part of a nucleate fiber, but bears no resemblance to it. It is an empty, nonprotoplasmic unit with walls bearing numerous large transversely oval bordered pits (Pl. II, Fig. 1). Frequently the pits are so large and numerous that there is space on the walls for only a reticulate network of secondary wall substance. Occasionally, however, they are small and fewer.

In a normal vessel element the single nearly round perforation is situated in the slightly oblique end. It is surrounded by a rather wide perforation rim, which reduces the area of the opening to two thirds or less of the area of the end. Small pits sometimes occur in the rim around the opening (Pl. I, Fig. 2). A lateral opening, in addition to the two end openings (Pl. II, Fig. 1) and long slanting ends with the perforations some distance from the extremities, have

been observed. Such variations from the typical form are infrequent but not exactly rare.

In transverse section the xylem-parenchyma cells are not easy to distinguish from the nucleate fibers because both have similar diameters, protoplasmic contents, and thickened walls. But their large pits are conspicuous in the end walls whenever these show in the section.

In longitudinal section some of the xylem-parenchyma cells are square and some are oblong (Pl. II, Fig. 3), and they are arranged in strands that are about as long as the vessel elements. The terminal cells of these strands have tapering or slanting ends. The pits in the transverse walls appear to be simple.

These parenchyma cells, which are distinctive among cells of this kind because of their thick walls and characteristic pitting, seem to ensheath the vessel elements almost completely, and, where vessel groups are close together, they constitute most of the tissue between them. The extent of continuity of the xylem-parenchyma tissue is difficult to determine because of the similarity of the cells in cross section to the nucleate fibers. Almost the only distinctive features of the parenchyma cells are the prominent pits in the cross walls and the slightly denser protoplasmic contents.

Xylem parenchyma is most abundant in the inner part of the secondary wood, especially opposite the primary xylem areas. Those cells near the primary xylem have noticeably thinner walls than the others.

The storied arrangement of the secondary xylem elements is a conspicuous feature in the radial section (Pl. II, Fig. 4). It can usually be seen extending from the inner limits of this tissue across the cambium and through the secondary phloem. It begins abruptly at the outer limit of the metaxylem.

DISCUSSION

The term "nucleate fiber" is proposed for the pointed secondary xylem elements in *Pelargonium zonale* in view of the apparent lack of any other suitable name for them. I have referred to such fibers as "substitute fibers," and among anatomical terms in current use this one is probably the most suitable. However, the Committee on Nomenclature of the International Association of Wood Anatomists has recommended that its use be discontinued because the cells that

it has always referred to are parenchyma cells. The committee has proposed the term "fusiform wood parenchyma" instead. In this particular instance, however, "fusiform wood parenchyma" is not an appropriate term to replace "substitute fiber" because it would be applied to cells that are essentially fibers and also because there are other cells present that do belong to the parenchyma category. Regardless of their shape, cells that the committee would designate as fusiform wood parenchyma do not belong to the fiber category. They are merely wood parenchyma chain initials that remain single cells.

The desirability of reinstating the term "substitute fiber" for the cells under consideration has been examined, but if it were adopted, it would then be used for something different from that for which it was originally proposed. Another objection to its use in this instance is that the nucleate fiber is not a cell that has replaced something, as the name "substitute fiber" would connote, but from the standpoint of both origin and structure is a genuine fiber. Its peculiarity is that it contains a protoplast. In most plants the protoplasts disappear as the final step in fiber development, and the cells become essentially nonliving entities. In *Pelargonium zonale* the process stops before the protoplast disintegrates.

Although thick-walled living cells are common in plants, their occurrence has never been comprehensively studied. This neglect is sharply reflected when one is confronted with such problems as the proper designation of the living fiber cells of *Pelargonium zonale*. Fibers, whether in the xylem or elsewhere, are almost always assumed to be empty, or, at least, to be nonprotoplasmic units. As a result, any thick-walled pointed cell is called a fiber, and by virtue of this assertion the cell is regarded as being nonliving. It may become necessary to reclassify some of these cells in the light of newer knowledge.

Some of the evolutionary trends in *Pelargonium zonale* are revealed in the anatomy of the stem. Although potted specimens look like herbs, the plants become shrubby when they are grown out of doors. Even potted specimens are atypical herbs in some respects. At least they depart from conventional textbook characterizations of herbs. These departures include retention of certain woody-plant traits, among which are the perennial habit and the meristems that continue to be active year after year. Then the

periderm, which may accumulate for several years without exfoliation, is obviously a holdover of a tissue which in the ancestor of the modern species produced detachable phellem.

The ancestor of *Pelargonium zonale* was probably a woody perennial of arborescent habit. Its secondary xylem in all likelihood consisted of wood fibers or fiber tracheids, parenchyma, vessels, and probably rays, although the fact that obscure rays occur throughout the family shows that the ordinary ray disappeared early in the evolutionary history of the family before the separate genera had become segregated. The only evidence in *P. zonale* that its ancestors ever possessed rays is the occasional presence of radially directed rows of xylem parenchyma cells.

It may also be assumed that the ancestor of *Pelargonium zonale* was a plant in which maturity of the wood fibers was attained when wall thickening was complete and the protoplasts had disintegrated. Mature fibers probably formed at only a very short distance inward from the cambium, as in most modern woody and shrubby plants. But during the ontogeny of the elongated xylem elements the protoplast persisted longer and longer in those cambial derivatives that served as fiber initials. Finally, the protoplasts failed to disappear, and the fibers were carried over into the mature wood as living cells.

The retention of living fibers in the mature wood of *Pelargonium zonale* cannot be interpreted as reversion to a primitive condition, but is a new development. Just what kind of cell first gave rise to the tracheary elements during the initial stages in the evolution of the vascular system, we do not know, but primitive plants in general are characterized by a high degree of uniformity in the kinds of tracheary elements which are consistently tracheids. The fiber tracheids, fibers, and vessels of higher plants are supposed to be modifications of the primitive and generalized tracheid. But not even in the lowest vascular plants (Psilophytales, Lycopodiales, and primitive Filicales) do the tracheids of the mature stem contain protoplasts. If, therefore, the condition revealed in *Pelargonium* were a reversion to the ancestral state, this plant would be expected to show intermediate stages between fibers and tracheids, or between vessels and tracheids. This, however, is not so. Instead, the types are sharply differentiated. In fact, the fibers and vessel elements are more unlike each other in *Pelargonium* than in most other plants. The remote ancestral condition, the condition that antedated the angiosperm level,

is probably revealed in the primary xylem, where we find both tracheids and vessels that are alike in size and wall sculpturing, and it is significant to note that the primary tracheids are nonprotoplasmic. The thick-walled, minutely pitted, pointed nucleate fiber of *Pelargonium zonale* is a highly evolved cell that has been derived from a wood fiber of the usual type. The vessels, on the other hand, have evolved along more usual lines. They show some distinctive features, but are essentially like those in other plants.

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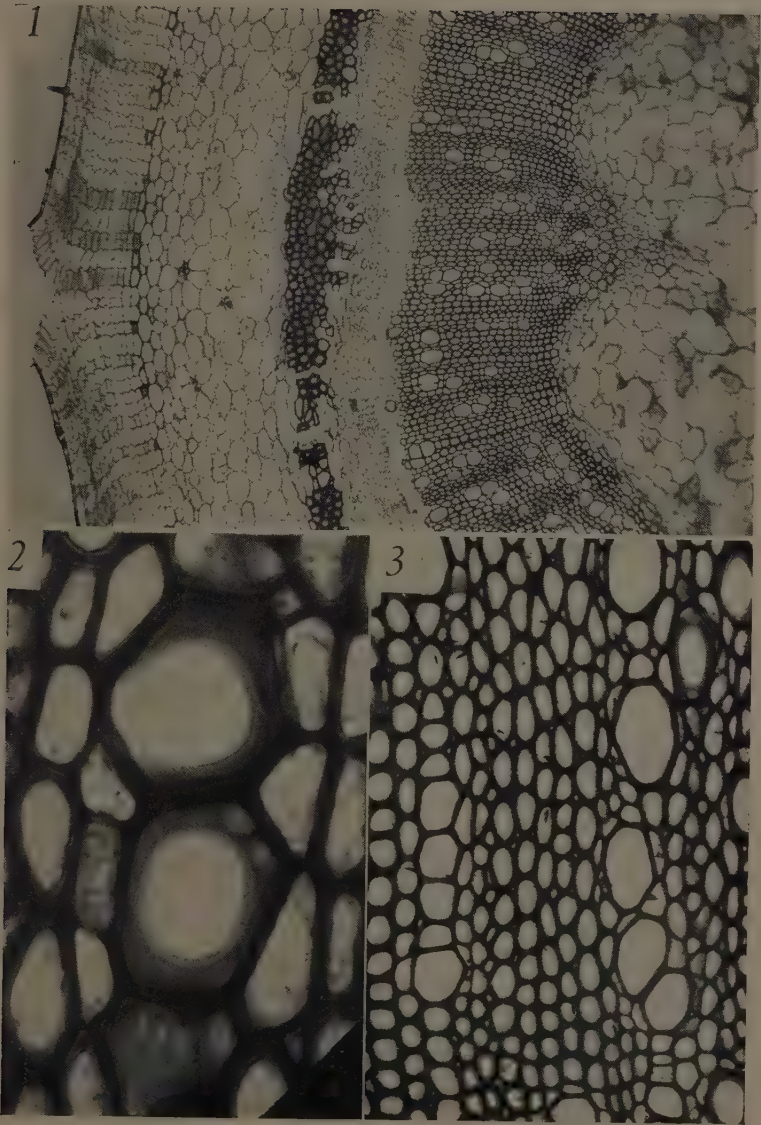
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EXPLANATION OF PLATE I

FIG. 1. Transverse section of portion of stem. $\times 30$

FIG. 2. Small portion of transverse section, showing the perforation rims of two vessel elements and adjoining parenchyma cells. The perforation rim of one element contains bordered pits. $\times 780$

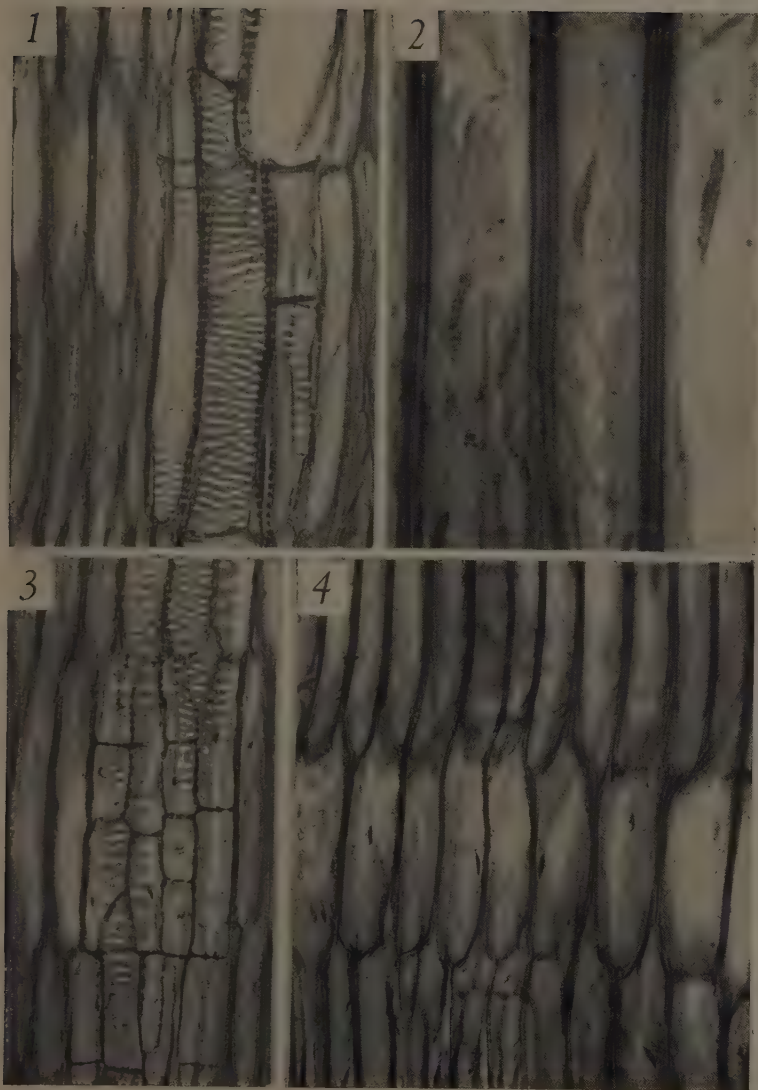
FIG. 3. Transverse section, showing "pore chains," intervening parenchyma, nucleate fibers, and absence of rays. $\times 110$



Pelargonium zonale

EXPLANATION OF PLATE II

- FIG. 1. Radial section, showing nucleate fibers (at left) and vessel elements with characteristic pitting. One vessel element contains a lateral perforation. $\times 130$
- FIG. 2. Enlargement of portion of three nucleate fibers, showing nuclei. $\times 800$
- FIG. 3. Radial section, showing a layer of wood parenchyma cells in the immediate vicinity of vessels not included in section. $\times 130$
- FIG. 4. Radial section, showing storied arrangement of nucleate fibers. $\times 130$



Pelargonium zonale

BOTANICAL AND ETHNOBOTANICAL STUDIES IN THE ALEUTIAN ISLANDS

I. ALEUTIAN VEGETATION AND ALEUT CULTURE*

THEODORE P. BANK, II

ANY study of primitive man should include an evaluation, as thorough as means permit, of his environment, including the various ecological factors brought into play by the terrain, climate, plants, and animals. During eighteen months of 1948-49 and during the summer of 1950 the writer had an opportunity to make phytoecological observations among the Aleutian Islands while undertaking for the University of Michigan a series of botanical and anthropological studies. Plant collections were made on seventeen of the islands, ranging from the Alaska Peninsula to Attu, the westernmost island. In another paper the writer has presented results of a series of phytoecological studies on old village sites in the Aleutians, made with the object of defining the vegetational differences resulting from human occupancy and of using these differences, if possible, as an aid to archaeology.¹ Since it contains a thorough description of the configuration, size, and vegetation of Aleutian village sites, there is hardly any reason to repeat any of the data. It is pertinent to note, however, that the sites were all coastal in situation, and presented the archaeological remains of primitive semisubterranean, sod-covered

* Contribution from the Department of Botany and the Botanical Gardens of the University of Michigan. I wish to acknowledge my sincere appreciation to H. H. Bartlett for his untiring efforts, as director of the Botanical Gardens, in support of the Aleutian Project during the four years that it has been active and for his help and advice in preparing this paper. Appreciation is also expressed to L. H. Jordal, a member of the 1949 expedition, who helped to identify the higher plants, and to A. Harvill, who identified the bryophytes. The research could not have been accomplished without the initial support of the Office of Naval Research and, later, that of the Michigan Memorial Phoenix Project, both of which contributed research funds. To the officers and men of the U. S. Navy, Army, Air Force, and Coast Guard and the personnel of the Alaska Native Service, all of whom furnished invaluable assistance in our field work, I am greatly indebted.

¹ This article will be published in elsewhere.

houses with whale-rib and driftwood supports. The Aleutians, prior to the coming of the white man, had populous villages located upon most of the more than sixty islands.

TOPOGRAPHY AND CLIMATE

The Aleutian Arc consists of about twelve large islands and fifty smaller ones, with more than a hundred offshore pinnacle rocks and islets upon which vegetation occurs. Descriptions of their rugged configuration, many active volcanos (Pl. II, Fig. 1; Pl. V, Fig. 2), treacherous reefs and rip tides, and uniformly inhospitable weather have been given by early Russian, English, and American explorers, by the anthropologists Jochelson (8, 9) and Hrdlička (5, 6), the naturalist William Dall (3, 4), and the botanist Eric Hultén (7), as well as by many casual visitors. Criticism of the islands' inhospitality has been perhaps most graphically presented by recent G.I.'s who found themselves stationed in the Aleutians. The writer will not attempt to repeat a full description of their topography and climate except to summarize certain meteorological data.² Table I presents figures for temperature, cloudiness, precipitation, and wind velocity for the period October, 1942, through September, 1948.

During the period for which data are at hand, February and March were consistently the coldest months of the year, and the lowest temperatures recorded were 11° and 12° F. In August and September, the warmest months, the highest temperature recorded was 75° F., in September. The mean daily maximum temperature during August and September was 54° F. Such uniformly temperate conditions no doubt made it possible for the Aleut to wear the clothing he did, which was, even in winter, primarily of gut, bird feathers, and woven grass.³

Scattered clouds to clear-sky conditions were most common during the winter months, but in no year was it clear during more than 1.8

² From records made available to the writer by the Officer in Charge of Meteorological Units, U. S. Navy and U. S. Air Force, Davis Air Force Base, Adak, Alaska, 1949.

³ Early descriptions by Sarychef, Tolstykh, Sauer, and Veniamenof as reported in Jochelson (9) and Hrdlička (6) state that the main clothing of the Aleut at about the date of Russian discovery was a long nightgown-like *kamleika* of seal and sea-lion gut. Some wore fur jackets of seal, sea-lion, and sea-otter skin. The women and children often wore feather jackets (especially of puffin feathers) and capes of woven beach grass. Most of the Aleut had no covering for the feet, even in winter.

TABLE I
CLIMATOLOGICAL DATA FOR ADAK, ALEUTIAN ISLANDS, AT SEA LEVEL DURING OCTOBER, 1942, THROUGH SEPTEMBER, 1948

Temperature: Degrees Fahrenheit											
Mean		Mean maximum		Mean minimum		Highest		Lowest			
40		44		36		75		11			
Sky condition: Percentage of time											
Clear		Scattered		Broken		Overcast		Obscured			
0.9		8.3		25.5		64.7		0.6			
Average monthly precipitation: Inches											
Precipitation											
Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
19.2	16.3	12.9	3.6	0.6	0.0	0.0	0.0	0.0	0.6	4.6	13.3
4.72	4.46	3.48	3.38	2.20	1.38	2.38	4.36	3.77	5.35	5.95	5.89
Wind velocity: Miles per hour											
Wind											
Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
15.8	16.5	16.5	15.2	14.5	11.9	12.8	13.7	14.9	16.8	14.7	15.9
89	100	85	72	58	60	64	58	81	69	79	84
SW	WNW	SW	W	W	SW	SW	SW	SW	SW WNW	SSW	SW

per cent of the time. The period of greatest overcast (78 per cent of the time) occurred during the months of June, July, and August. Our field parties recorded for the middle part of the Aleutian Chain a total of less than 60 hours of sunshine for the three months, July, August, and September during the three years 1948-50 (Bank, 1)—20 hours a year! Aleutian winds are uniformly high and variable in direction. Gusts are frequent, especially during October and November and again during January, February, and March, often reaching 120 miles per hour. Wind velocities (Table I) were taken at a station less than 50 feet above sea level, as were the other weather observations. Although the mountaintops may sometimes extend above the cloud layer and receive more sunlight, they are most of the time bathed in fog and clouds. Especially during the summer months the interior parts of the islands are somewhat wetter than the shore, except on the higher slopes where desiccating winds have a counter-acting effect. More snow accumulates in the interior valleys than at the shore. Wind velocities seem consistently higher as one leaves the sea to journey inland, and during the winter the ridges are constantly swept bare of snow. Winter walking in the alpine regions is almost impossible. Lower temperatures than any recorded at sea level prevail even a few miles inland, and winter temperatures of mountain ridges go considerably below 0° F.

The high winds, more than any other factors, have probably been responsible for restricting the Aleutian flora and have greatly modified the way of human life on the islands. Dressed only in flimsy clothing and usually barefooted, the Aleut was probably unable to journey very far above the beach during the winter months. Jochelson (8) and Hrdlička (6) give the impression that maintaining the ancestral custom of gaining their livelihood from the resources of the sea accounted for their living at the shore.

PLANT HABITATS

In an effort to describe the vegetational features of the Aleutians, the writer has studied the distribution of the major plant habitats. Although there are additional microhabitats which will repay study, those which are sufficiently extensive and typical to show by mapping have been classified. Beginning at the seashore and proceeding inland, we find a series of sites which occur with minor variation on practically every island along the Chain. A schematic profile of

two typical islands is presented in Figure 1 to illustrate the habitat relations. Beginning with the sea the habitats are:

- I. Shoreline: everywhere rugged and rocky, with a few large, protected harbors but with many smaller bays, inlets, coves, and bights (Pl. I, Fig. 1).
 - A. Reef: usually of wave-cut basalt extending from every point of land and present also in many of the bays; inhabited by abundant edible Algae and animals.
 - B. Shore wall (cliff): wave-cut, often presenting tall pinnacle rocks and offshore islets; in places rising directly from the sea; elsewhere a rampart of high cliffs behind a narrow beach; inhabited by a myriad sea-bird population.
 - C. Beach: generally of cobble and strewn with huge boulders, but frequently (usually in bays and inlets) of gray to black sand.
 - D. Grass-thicket zone:
 1. Marginal ridge: often several such ridges or old beach lines lying in succession behind the present beaches; thick with grasses.
 2. Grass hummock: highly irregular, hummocked surface thickly overgrown with grasses, many edible plants, and plants used in weaving.
 3. Intermarginal depression: behind the marginal ridge; marshy during some seasons and containing a number of the medicinal plants. If there are several parallel marginal ridges, there are corresponding parallel inter-ridge depressions.
- II. Lower grass meadow: extending from above the beach to varying altitudes but characterized by a heavy growth of grasses, ferns, and other lush vegetation, much of it used by the ancient Aleut.
 - A. Stream valley: broad and U-shaped on larger, mountainous, islands; practically nonexistent on the lower, platform, islands (Fig. 1; Pl. I, Fig. 2).
 1. Stream margin: wet and usually rocky. Streams and lakes are abundant in the Aleutians; larger streams near the sea contain many salmon and trout during the summer and early fall.
 2. Ravine bank: steep, fern-covered, and interfering with inland travel (Pl. III, Fig. 1).
 3. Drainage flat: wet area above stream but below surrounding stream valley slopes and receiving drainage from them.
 4. Knoll or plateau: usually comparatively dry and covered with a thick mat of *Empetrum*, mosses, and lichens, together with many edible berries (Pl. IV, Fig. 1).
 5. Meadow slopes: sometimes steep and usually dissected by ravines, which, with drainage flats, make walking across them difficult.
 - B. Lake depressions: especially abundant on the platform islands and occurring even at high altitudes wherever shelves or other flat extensions of the mountain are to be encountered (Pl. IV, Fig. 2).
 1. Shallow water flat: depth of water varies considerably during year.
 2. Marginal ooze: marshy transition zone between water and higher ground. (Here are many medicinal plants!)
 3. Drainage slopes: wet and usually gentle slope rising away from the lake to dry knolls, plateaus, or better-drained meadow slopes.

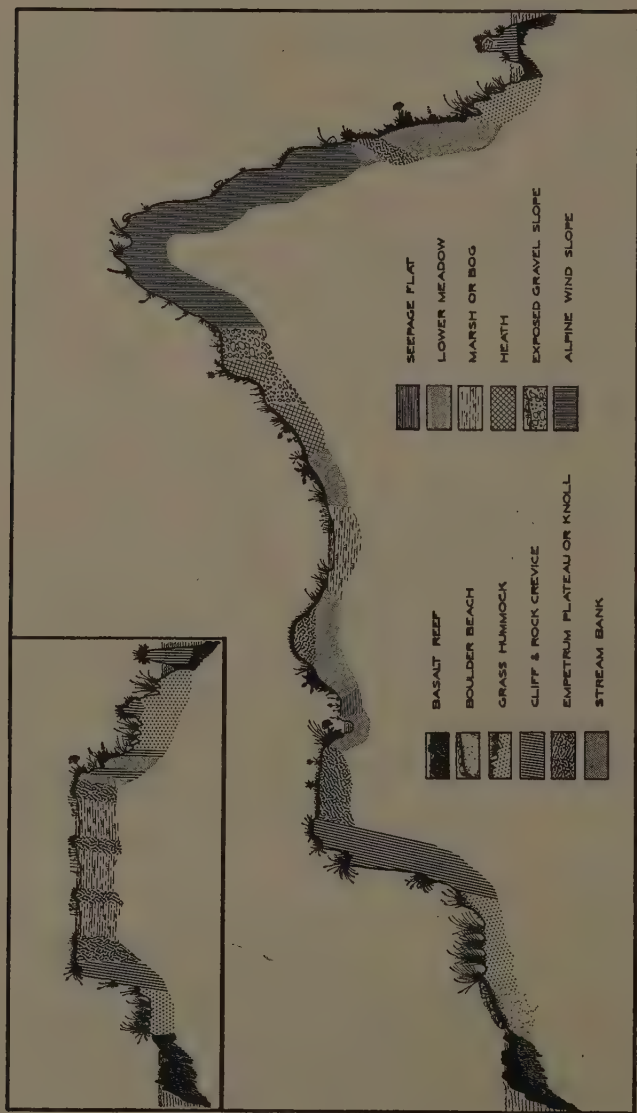


FIG. 1. Diagram representing the topographic relations of the chief habitats on the two main types of island in the Aleutian chain, namely, the plateau island (at upper left) and the mountainous island (below). The physiognomy of the vegetation is hinted at by the marginal profile. Adjacent to each part of the profile is a symbolic indication of the corresponding plant association or community, which is to be interpreted by reference to the plant lists given in the text

- C. Marsh or boggy area: usually small but sometimes extensive, especially in broader stream valleys (Pl. III, Fig. 2).
 - 1. Mudflat: usually drying up during certain periods.
 - 2. Standing water marsh: unstable ground often deep enough to mire heavy vehicles; contains a number of medicinal plants.
 - 3. Seepage slopes: often at high altitudes in the middle of dry meadows or heath areas. These are like running sores in the mountain slopes where underground drainage comes to the surface.
- III. Rock cliff: at the upper limits of the meadows, often successive vertical walls rising from the stream valleys and ravines, and effective barriers to inland travel.
 - A. Rock-face niches and crannies: crevice soil deposits and shelf extensions support a varied plant growth.
 - B. Seepage slopes: wet, alga- and moss-covered areas usually at the base of a cliff or in the bottoms of crevices.
- IV. Wind slopes: higher slopes where wind is a dominating factor in determining the vegetation.
 - A. Heath zone: covers large areas of the islands where the high winds have a desiccating effect even if the relative humidity is high.
 - B. Exposed gravel areas: eroded exposed soil or gravel; found frequently on narrow terraces at upper altitudes.
 - C. Talus: usually barren.
 - D. Alpine mountaintops: extremely rocky, windy, and cold; with lichens, moss cushions, and thin *Empetrum* mat (Pl. V, Fig. 1-2).
- V. Special habitats:
 - A. Bird mound: common on most ledges and hills near the sea; formed by vegetation growing in the droppings of numerous sea birds through centuries (Pl. VI, Fig. 1).
 - B. Steam jets and hot springs: fairly common on slopes of active volcanoes and along the seashore below them (Pl. VI, Fig. 2).
 - C. Salt marsh: infrequent.
 - D. Village sites: along coasts of all islands, especially in bays, on points of land, and isthmuses.
 - E. Glacial margin: occurs in upper valleys of larger, mountainous islands.

Shoreline Vegetation

Sea cliffs and soil patches among beach boulders contain growths of lichens and certain mosses, for example, *Pohlia cruda* (H.) Lindb., *Plagiothecium Roseanum* (Hype.) Bry. eur., and *Brachythecium albicans* (H.) Bry. eur.; species of *Poa*, *Potentilla villosa* Pallas ex Pursh, *P. nana* Willd. ex Schlecht., *P. palustris* (L.) Scop. (principally east of Unalaska), and *Saxifraga bracteata* D. Don.

Between the boulder zone and the grass hummocks there are usually small patches of gray to black sand or small cobbles and driftwood with at least scattered growths of *Cochlearia officinalis* L.

and *Lathyrus maritimus* (L.) Bigel., as well as a few grasses. Above this and sometimes encroaching upon it will be found the very common grass hummocks of Aleutian beach slopes. These hummocks, principally of *Elymus arenarius* L. ssp. *mollis* (Trin.) Hult., are often extremely high. They may be taller than a man's head and present a real problem to one attempting to cross them. Such an attempt usually results in frequent tumbles into the narrow deep spaces between the unstable hummocks. Associated with *Elymus* are a number of mosses and higher plants, among which the following are the most common: *Lathyrus maritimus* (L.) Bigel. (on the seaward margin), *Senecio Pseudo-Arnica* Less. (often growing three feet high), *Honckenya peploides* (L.) Ehrh., *Festuca rubra* L. (very common in the Aleutians), *Claytonia siberica* L., *Cerastium Fischerianum* Sér., *Phleum alpinum* L. var. *americanum* Fournier, *Mertensia maritima* (L.) Gray, *Stellaria calycantha* (Ledeb.) Bong., *Clayopodium Bolanderi* Best, and other mosses.

When hummock zones are lacking, their place is usually taken by dense *Elymus*-*Phleum* stands on uneven drained slopes or by areas of direct transition to a lower meadow, heath area, or cliff.

Lower Grass-Meadow Vegetation

Above the beaches, except where cliffs occur, there is usually a series of habitats which may be conveniently grouped and termed "lower grass-meadow." Each stream valley, for instance, presents a sequence of habitats from the water's edge to higher ground. In the water and attached to rocks may often be found *Fontinalis neomexicana* Sull. & Lesq., *Ranunculus aquatilis* Schlecht. var. *capillaceus* Ledeb., and *Myriophyllum spicatum* L. The writer collected these aquatic species on Umnak, Adak, and Atka islands.

Growing along the stream margin are *Streptopus amplexifolius* (L.) DC., *Linnaea borealis* L., *Juncus balticus* Willd., various grasses, ferns, *Carex* species, and, especially in the western Aleutians, *Vetrarium album* L. ssp. *oxysepalum* (Turcz.) Hult. and *Veronica americana* Schwein. We also found on Attu scattered clumps of *Sorbus sambucifolia* (Cham. & Schlecht.) Roem. *Leptarrhena pyrofolia* (D. Don.) Sér. is found in the spray of waterfalls but less commonly west of Adak, and *Petasites frigidus* (L.) Fries occurs scattered next to high mountain streams. Among the stream-margin mosses are found

Hylocomium splendens (H.) Bry. eur., *Rhytidiadelphus loreus* (H.) Warnst., *R. squarrosus* (H.) Warnst., and *Antitrichia curtipendula* (H.) Brid.

Growing on the steeper banks of streams (Pl. III, Fig. 1) are *Streptopus*, various ferns, among them *Athyrium Filix-femina* (L.) Roth. and *Dryopteris oreopteris* (Ehrh.) Maxon, as well as *Claytonia siberica* L., and *Artemisia*, especially *A. unalaskensis* Rydb. var. *aleutica* Hult. Where the bank is well drained there are found *Lycopodium clavatum* L., *Anaphalis margaritacea* (L.) Benth. & Hook. var. *occidentalis* Greene, *Achillaea borealis* Bong., and *Epilobium angustifolium* L. var. *macrophyllum* (Hausskn.) Fern. as well as *E. anagallidifolium* Lam. (not too common on all islands). Also occurring here are *Galium Aparine* L., which is often a seashore plant, *Antennaria dioica* (L.) Gaertn. (scattered), and *Rhinanthus groenlandicus* Chabert. *Carex macrochaeta* C. A. Meyer is the most common sedge. Especially in the spray near falls and growing in seepage areas are *Saxifraga punctata* L. ssp. *insularis* Hult., and *Leptarrhena pyrolifolia* (D. Don.) Sér. Occurring on dryer banks are *Geranium erianthum* DC., *Aster peregrinus* Pursh (*Erigeron*), which also is frequently found at higher altitudes, and such grasses as *Festuca rubra* L., *Agrostis* species, and *Deschampsia beringensis* Hult., which are common across the Chain. *Rhododendron kamtschaticum* Pallas and *Vaccinium ovalifolium* Smith are fairly common along the steep, dryer mountain-stream valleys, the latter being more restricted to the western islands.

Almost universally there is present above the stream a flat, wet area which collects drainage from the slopes around it (Fig. 1). This flat usually itself drains into the stream and seldom has standing water, although it is almost continually wet. Commonly found here are several species of *Platanthera*, especially *P. hyperborea* (L.) Lindl., *P. dilatata* (Pursh) Lindl., and *P. tipuloides* (L. f.) Lindl., the latter occurring primarily in the western islands, but rarely elsewhere. *Orchis aristata* Fisch. ex Lindl., *Fritillaria camschatcensis* (L.) Ker-Gawl., *Polygonum viviparum* L., *Pinguicula vulgaris* L., *Aster peregrinus* Pursh, *Epilobium Behringianum* Hausskn., and other plants also inhabit these drainage flats. Occasionally *Cypripedium guttatum* Swartz is found here. Clusters of this species occurred in two widely separated localities, Adak and Unalaska, but

it has been reported from other islands. Iris, Arnica, sometimes Mimulus, *Angelica lucida* L., low grasses, liverworts, and mosses of various types frequently inhabit the flats.

In places covering large areas, especially in the broader stream valleys, but elsewhere separating the stream margin from the dry Empetrum knolls above by only a narrow strip, are to be found the fairly well drained, thickly carpeted valley meadows. These are usually gentle to moderately steep slopes, covered with tall grasses, umbellifers, and invaders from the heaths above and the wet habitats below. *Erigeron*, *Platanthera*, *Fritillaria*, and *Epilobium* invade from the stream valleys and from above have come such species as belong more properly to the alpine habitats, for example, *Lupinus nootkatensis* Donn ap. Sims, *Anemone narcissiflora* L. var. *villosissima* DC., and others. Thickly covering these valley meadows are *Calamagrostis Langsdorffii* (Link) Trin., which is perhaps one of the most common grasses in the islands, along with *Deschampsia beringensis* Hult., which runs a close second. *Heracleum lanatum* Michx., *Angelica lucida* L., *Pedicularis Chamissonis* Steven., *Anaphalis margaritacea* (L.) Benth. & Hook. var. *occidentalis* Greene, *Geum calthifolium* Menzies, *Aconitum kamtschaticum* Pall. & Schlecht., *Epilobium angustifolium* L. var. *macrophyllum* (Hausskn.) Fern., *E. Behringianum* Hausskn., and *E. glandulosum* Lehm. make up a large part of this vegetation. *Epilobium latifolium* L. and *Castilleja unalaschcensis* (Cham. & Schlecht.) Malte occur abundantly, especially in the eastern islands, whereas species primarily of the western islands include *Senecio palmatus* (Pall.) Ledeb., *Sorbus sambucifolia* (Cham. & Schlecht.) Roem., *Chrysanthemum arcticum* L., and *Cirsium kamtschaticum* Ledeb. ex DC. Occurring in scattered patches is *Trientalis europaea* L. subsp. *arctica* (Fisch.) Hult., and *Ranunculus occidentalis* Nutt. subsp. *insularis* Hult. is fairly common, especially near streams. *Maianthemum dilatatum* (Howell) A. Nels. & T. Macbr. is found as part of the valley-meadow vegetation wherever drainage is poor.

Hultén has presented a profile of characteristic vegetation bordering lakes and extending from them to higher and drier ground. It is hardly necessary to repeat his listing. Many species bordering streams also occur near the lowland lakes, especially species of *Carex*, *Scirpus*, *Juncus*, and *Polygonum* (Pl. IV, Fig. 2). *Caltha palustris* L. is often found along the lake margins at least as far west as Tanaga.

Petasites frigidus (L.) Fries has also been found fairly commonly, especially at higher altitudes.

Common throughout the Aleutians are boglike areas in the sides of hills both at lower altitudes and in the alpine regions. These are seepage slopes and are essentially oozing underground drainage from the hills above. They often occur in the center of an otherwise dry heath slope. Their vegetation consists mainly of mosses and liverworts, but frequently found in them are *Mimulus guttatus* DC. (at low altitudes), *Viola Langsdorffii* Fisch. in DC., *Leptarrhena pyrofolia* (D. Don.) Sér. (not common in the west), *Pinguicula vulgaris* L., *Rumex Acetosella* L., and *Saxifraga punctata* L. subsp. *insularis* Hult. Mosses of these seepage areas include *Sphagnum capillaceum* (Weis.) Schrader., *S. Girgensohnii* Russ., *Rhytidiadelphus triquetrus* (H.) Warnst., *Girgensohnia ruthenica* (Weim.) Kindb., *Plagiothecium undulatum* (H.) Bry. eur., *P. Muellerianum* Schimp., *Pleurozium Schreberi* Mitt., *Dicranum Bonjeanum* De Not., *D. majus* Smith, *Brachythecium washingtonium* Grout, *Cirriphyllum piliferum* Grout, *Mnium punctatum* H., *Oligotrichum parallelum* (Mitt.) Kindb., and *Bryum turbinatum* (H.) Schwgr. Such zones of unstable, extremely wet and boggy ground often require long detours when one is botanizing in meadows above the beaches.

Marsh vegetation closely resembles that of the lake margins, and it is true that many Aleutian marshes are lakes which have partially dried. They are common along the shores of bays and inlets, at the mouths of larger streams, and along the bottoms of broad stream valleys (Pl. III, Fig. 2). Others occur frequently, as at Atka, on higher ground, where a flat area is surrounded by hills. Most often they are found to contain a central "puddle" or small stagnant pond. Such areas are very common west of Adak, where many of the islands are essentially plateaus rising above the sea, whose surfaces are all marshland dissected by occasional grass hummocks or moss knolls. There are no true bogs in the Aleutians of the type found extensively in Alaska, Canada, and north-central United States. Floating sphagnum mats are not to be found. The areas most closely resembling bogs are the seepage slopes already described, but they are usually not deep; they result from hillside drainage and fluctuate in size with changing weather conditions.

The vegetation of the marshes varies according to the amount of standing water present. Typically, however, one finds *Polygonum*

viviparum L., *Eriophorum medium* Anders., *Carex rariflora* (Wahlenb.) Smith subsp. *stygia* (Fr.) N. J. Anders., *Scirpus caespitosus* L., *Iris setosa* Pall. ex Link, *Geum calthifolium* Menzies, *Aster peregrinus* Pursh, *Conioselinum Gmelini* (Cham. & Schlecht.) Coult. & Rose, *Matricaria matricarioides* (Less.) Porter, *Plantago macrocarpa* Cham. & Schlecht., *Juncus ensifolius* Wikstr. (more common toward the east), *Juncus balticus* Willd., and *Caltha palustris* L. The writer found occasional areas where *Menyanthes trifoliata* L. was common. This plant was considered by the Aleuts of Nikolski an extremely powerful medicine for stomach disorders.

Characteristic of the better-drained hilltops at lower altitudes is the sometimes thick *Empetrum*-moss-lichen mat (Pl. IV, Fig. 1). These mat areas are easily picked out from the air, since they show up as much darker splotches on most hilltops (Pl. I, Fig. 2). During the rains of spring and early fall the *Empetrum* mats are like water-soaked sponges, and water squirts from them when they are stepped upon. Although never thoroughly drying out, they are, nevertheless, dry enough at other times to provide a truly comfortable mattress for a tired hiker. Their vegetation includes *Empetrum nigrum* L., *Lycopodium clavatum* L., *L. sabinaefolium* Willd. var. *sitchense* (Rupr.) Fern., *L. annotinum* L., *L. Selago* L., and *L. alpinum* L. (the last species at higher altitudes). Lichens, especially *Cladonia*, form much of the mats, as do mosses, including the following: *Brachythecium albicans* (H.) Bry. eur., *Rhacomitrium lanuginosum* (H.) Brid., *Pogonatum alpinum* (H.) Brid., and others. *Phyllodoce aleutica* (Spreng.) A. Heller, *Loiseleuria procumbens* (L.) Desv., and *Vaccinia*, especially *Vaccinium uliginosum* L. and *V. Vitis-Idaea*, make up part of the association, although quite often *Vaccinium* is completely lacking. Also found as members of the mat are *Campanula lasiocarpa* Cham., *Antennaria monocephala* DC., *Coptis trifolia* (L.) Salisb., *Trientalis europaea* L. subsp. *arctica* (Fisch.) Hult., *Cornus suecica* L., *Linnaea borealis* L., *Veronica Stelleri* Pall. ex Spreng., *Cassiope lycopodioides* (Pall.) D. Don, and *Rubus stellatus* J. E. Smith. *Rubus Chamaemorus* L. is common in the western islands.

ROCK-CLIFF VEGETATION

At the bases of low-altitude rock cliffs there is usually to be found a seepage area with a rank growth of ferns, including *Athyrium*

Filix-femina (L.) Roth., *Cystopteris fragilis* (L.) Bernh., and sometimes *Botrychium* sp. and *Dryopteris Linnaeana* C. Chr. Also found here are *Claytonia sibirica* L., *Saxifraga bracteata* D. Don, *Selaginella selaginoides* (L.) Link, *Draba hyperborea* (L.) Desv., *Barbarea orthoceras* Ledeb., and *Saxifraga rivularis* L., the last being most common at higher altitudes in flat, wet-mud patches. Hultén thinks that *Barbarea* occurs only close to villages, but the writer has found it on uninhabited islands and in areas far inland from villages. Mosses of the wet cliffs include *Hylocomium splendens* (H.) Bry. eur., *Rhytidiadelphus loreus* (H.) Warnst., *R. squarrosus* (H.) Warnst., *R. triquetrus* (H.) Warnst., *Antitrichia curtipendula* (H.) Brid., *Drepanocladus uncinatus* (H.) Warnst., and others which occur regularly as part of the hillside-seepage vegetation.

WIND SLOPES

Beginning at no definite altitude is the very widespread alpine region of the Aleutians. It often extends down into the lower stream valleys and occurs close to the shore, although more commonly it is not to be found except inland. The entire vegetation is in an unstable condition. Major fluctuations have slowly occurred since the departure of the icecaps, which covered each island during the Pleistocene. Minor fluctuations continually occur today. They can be seen in the invasions, withdrawals, and reinvasions of certain plant associations, as, for example, in the shifting back and forth between marsh and meadow vegetation. Although longer than seasonal, these shifts are oscillatory and are brought about by periodic surpluses of moisture. Particularly heavy winter snowfalls often cause changes in areas from meadow to marshland, with a corresponding shift in vegetation. Many Aleutian plants show a surprising adaptability as well as capacity for invading newly available areas quickly. For example, Glacier Creek valley of Great Sitkin Island was visited by the author in 1949 and found to be choked with ice and snow. The newly ice-free areas were barren of plant growth. By the same time the following summer these areas were dotted with lichens, various mosses, sprouts of adventuring *Lupinus nootkatensis*, *Hieracium* sp., *Poa* sp., *Carex* sp., and a single *Campanula*. Hultén mentions the unusual pioneering ability of *Senecio Pseudo-Arnica*; it has invaded in numbers the famous Bogoslov Island, which has appeared above the sea, disappeared, and appeared again since

Russian times in the Aleutians. Hultén also observes that the Aleutian flora is largely the same as that of Kamchatka, with the addition of American elements throughout, but its associations are much less stable.

The alpine meadow is almost nonexistent, being merely a transition zone, usually narrow, between the lower or subalpine meadows and the alpine heath slopes above. *Calamagrostis Langsdorffii* (Link) Trin., *Geranium erianthum* DC., *Salix crassijulis* Trautv., *S. ovalifolia* Trautv., *Anemone narcissiflora* L., *Aster peregrinus* Pursh and other plants make up this transitional complex. Not infrequently the mountain-stream valleys consist entirely of this vegetation, with additional *Lycopodium* species, *Rhododendron kamtschaticum* Pallas, *Cornus suecica* L., and various short grasses and lichens.

The heath slopes of the island cover comparatively large areas and are truly the windswept, desolate, rocky, barren-appearing regions envisioned as typical of the Aleutians by most nonvisitors. Temperature differences between the coast and the inland heath slopes are sometimes fairly great, but apparently not so great as to cause large vegetational differences. It is, rather, that the high winds which constantly blow across the ridges and higher slopes of the interior are the primary factor in the vegetational make-up of these places. Despite the uniformly high humidities (85–95 per cent) in the Aleutians, the constant circulation of air caused by continual strong winds makes for desiccation of plant tissues. Hultén has appropriately called attention to the “wind planes,” areas over which the movement of the wind is not retarded by the relatively smooth surface of the greater part of the vegetation. Even a pocket in the vegetation a few inches deep is relatively out of the wind and therefore constitutes a considerably different microhabitat. I have chosen to call “wind slopes” those areas over which there is a “wind plane” at the general surface of the mat or heath vegetation, which has so profound a drying effect that it determines the aspect and form of the plant association. Where *Salix* is the only larger woody plant, it is procumbent, of “krummholz” form (Fig. 2).

Characteristically moulded by the wind planes are extensive areas of *Empetrum nigrum* L., *Cladoniae*, and *Salices*, which cover the ground as a weatherworn carpet. Many lichens and mosses make a part of this carpet, together with scattered growths of the following: *Lycopodium clavatum* L., *L. alpinum* L., *L. Selago* L.,

Carex rariflora (Wahlenb.) Smith. *C. circinnata* C. A. Meyer, *C. nigricans* C. A. Meyer, *Tofieldia coccinea* Richards., *Campanula lasiocarpa* Cham., *C. dasyantha* M. a Bieb., *Cassiope lycopodioides* (Pall.) D. Don, *Antennaria monocephala* DC., *Coptis trifolia* (L.) Salisb., *Loiseleuria procumbens* (L.) Desv., *Calamagrostis purpurascens* R. Br., *Linnaea borealis* L., various *Vaccinia*, and clumps of *Lupinus*

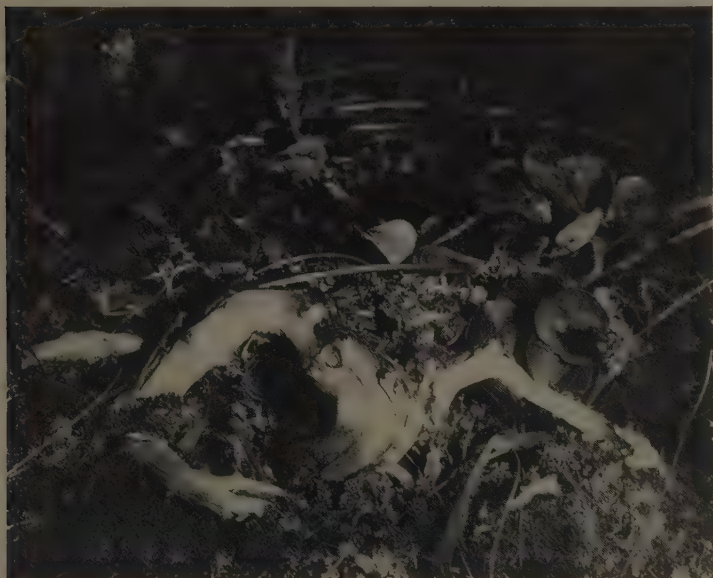


FIG. 2. Weathered trunk of a procumbent *Salix* (*S. crassijulis* Trautv.?) showing the usual "krummholz" form of plants subjected to high winds, including all the scattered willows in and above the *Empetrum* mat

nootkatensis Donn ap. Sims., and *Anemone narcissiflora* L. var. *villosissima* DC.

Within the heath zones are numerous moss- and lichen-covered boulders which have rolled from the eroding peaks and cliffs. Among the mosses of these special minute habitats are: *Hypnum callichroum* Brid., *H. Dieckii* R. & C., *Mnium punctatum* H., *Rhacomitrium aciculare* Brid., *R. lanuginosum* (H.) Brid., and *Pohlia cruda* (H.) Lindb.

Also characteristic of the windswept slopes in the interiors of the

Aleutians are eroded patches of gravel and rubble, which often form terraces of bare soil and rock on an otherwise heath-covered slope. Invading these highly unstable areas are scattered growths of *Polygonum viviparum* L., *Campanula lasiocarpa* Cham., *C. dasyantha* M. a Bieb., *Salix*, *Primula cuneifolia* Ledeb., *Antennaria* sp., *Barbarea orthoceras* Ledeb., *Cardamine umbellata* Greene, *Luzula nivalis* (Laest.) Beurl. var. *latifolia* Kjellm., *Petasites frigidus* (L.) Fries, and, less generally, *Oxyria* and *Saxifraga*. Pioneering lichens and mosses tend to invade first. The wind-eroded stems and roots of *Salix* present a picture like that of tangled diminutive beach driftwood protruding from sand, but the hardy willows manage to remain alive despite the windstorms and gravel blasting characteristic of these areas (Fig. 2). Other plants will grow when somewhat protected by the willows.

SPECIAL HABITATS

Inasmuch as the writer expects to treat such special habitats as steam jets, volcano craters, bird mounds, salt marshes, and village sites at a later date, they are passed over with mere mention in the present paper. Steam jets and hot springs have universally been disregarded by collectors in the Aleutians, but they possess a unique and interesting algal flora. They were used by the Aleuts as a source of ochres and, occasionally, for boiling food. In the steam of jets they placed strips of driftwood (*Taxus*) to be bent for the construction of boat frames. The writer made observations and collected algae and mineral specimens from such localities on Umnak, Kagamil, Atka, and Great Sitkin islands.

ALEUT CULTURE AND ALEUTIAN PLANTS

The Aleuts were well adapted to living along the peripheries of the islands, being almost exclusively a maritime people (Collins, 2). They seldom journeyed inland and did not seem to care much for higher ground. According to early Russian accounts, they were actually adapted physically more to paddling great distances cramped in skin boats than to walking even moderate distances overland. When they made trips into the mountains, they were usually in search of volcanic ochres and certain types of rock used in the manufacture of weapon points.

Their food supply was from either the sea or its margin. Aside

from sea mammals and fish, which comprised their main diet, abundant kelp, *Fucus*, *Ulva*, and small animals were gathered for food from the shore waters and reefs. Kelp was utilized in the making of fish lines. Along the shores grew species of *Senecio*, *Heracleum*, *Angelica*, *Claytonia*, *Cochlearia*, *Conioselinum*, *Achillaea*, and more than twenty other plants which were used extensively for food and medicine. *Lathyrus*, *Elymus*, and other grasses were employed in weaving. *Aconitum* was used by at least some of the Aleut villagers as a source of fish and whale poison. Although certain medicinal plants, such as *Matricaria*, *Caltha*, and *Menyanthes*, occurred chiefly in swampy areas, these were usually close at hand and did not necessitate a major trek inland. Berries were common in the lowland meadows. *Rubus*, *Vaccinium*, and *Empetrum* mats were thickest nearer the shore and thin at higher altitudes.

Soil depth and drainage, which were important considerations in the choice of sites for villages, were better along the shores of the islands than inland. From the sea came whale ribs, which were used as supports for the sod roofs of the Aleut barabaras. From the sea also came the Aleut's wood, for the only source was driftwood. From Asia he received as drift such woods as *Taxus cuspidata* S. & Z., which he bent into ribs for his boats. America contributed *Salix*, *Chamaecyparis*, *Taxus*, *Picea*, and other woods. The Aleut used cedar for masks; cottonwood for carving and, later, for smoking salmon; and birch for fashioning hats.

The sea not only furnished the Aleut with his livelihood, but also provided him with an avenue of escape from enemy attackers from neighboring islands. Even the flattest islands have raised portions near the beach which served as lookout posts for enemies and sea mammals. Caves, which were used for burials by at least some groups during a portion of Aleut existence among the islands, are far more common along the shores than inland. And were the Aleut to journey very far inland on his island, he would find the winds too violent for sustained comfort, and so he, like most modern visitors to the Aleutians, avoided the upland.

It would seem that the Aleuts were limited to their maritime existence by more than merely their cultural inheritance from a mainland source. That they were a maritime people prior to arriving in the Aleutians seems probable, but the Aleutian environment, with its climatic, vegetational, animal, and topographic limitations,

must have played no small part in the ultimate shaping of their way of life. Just how radically their customs were modified by the total impact of ecological factors remains, of course, indeterminable up to the present, but will to some degree be revealed, it is hoped, by the archaeological sequences in old village sites.

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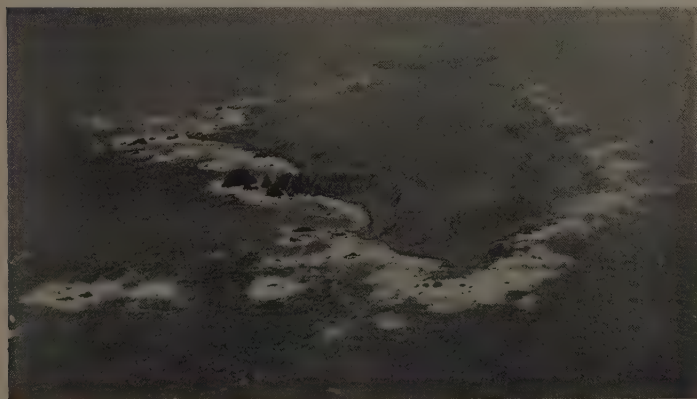
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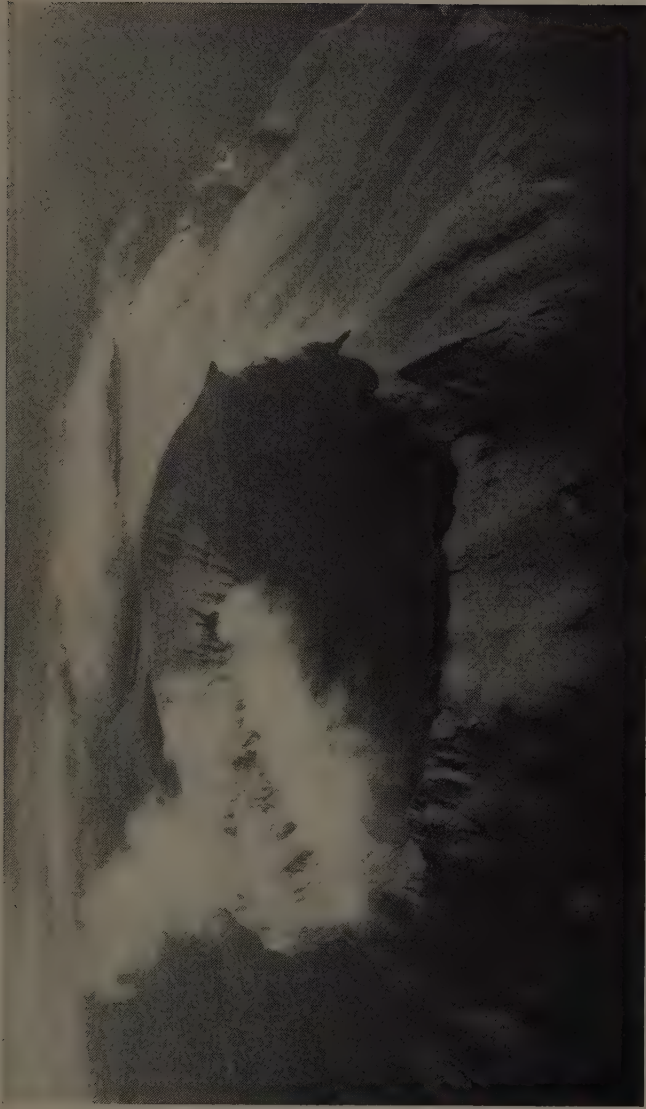
Official U. S. Navy photograph

FIG. 1. Western tip of Attu Island, showing extremely mountainous terrain and rugged coastline common to the larger Aleutian islands. Although there are no active volcanoes on Attu, these are a prominent feature of the eastern Aleutians



Official U. S. Navy photograph

FIG. 2. Ilak Island, an example of the Aleutian platform island. Such flat, usually small islands are found west of Adak. The vegetation of the central portion of the plateau is mainly *Empetrum* mat, which is surrounded by a narrow belt of meadow vegetation



Crater lake on Kasatochi Island. Many ancient craters remain as evidence of past volcanism. There are still approximately thirty-five active volcanos on the Aleutian Arc

Official U. S. Navy Photograph



FIG. 1. Stream ravine, wet and generally steep, with rank growth of ferns, grasses, and high-growing umbellifers



FIG. 2. Lowland marsh, where commonly occur medicinal plants once used by the Aleut



FIG. 1. Detail of an *Empetrum* mat. *Empetrum nigrum*, lichens, mosses, and a number of large-flowered plants, such as *Campanula* (shown), occur as part of this knoll and plateau plant association



FIG. 2. Highland lake habitat, showing characteristic marginal stands of sedge



FIG. 1. Alpine mountaintop. Such heights are usually boulder-strewn, with vegetation restricted by climatic factors, especially wind, mainly to lichens and mosses



FIG. 2. Great Sitkin Volcano, July, 1948, an example of the physiognomy of many Aleutian peaks

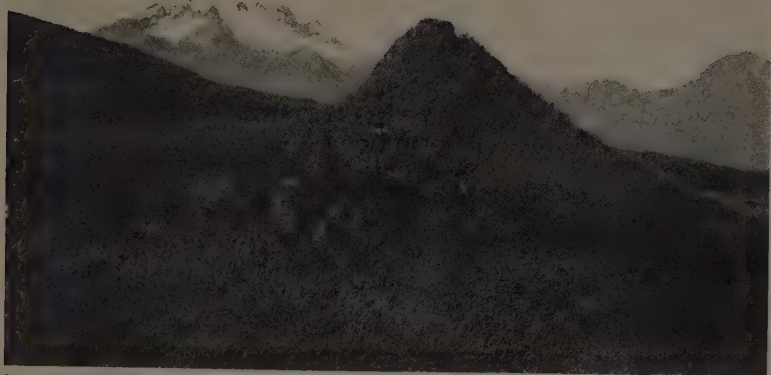


FIG. 1. Bird mound. Such mounds are common along seashore cliffs throughout the Aleutians

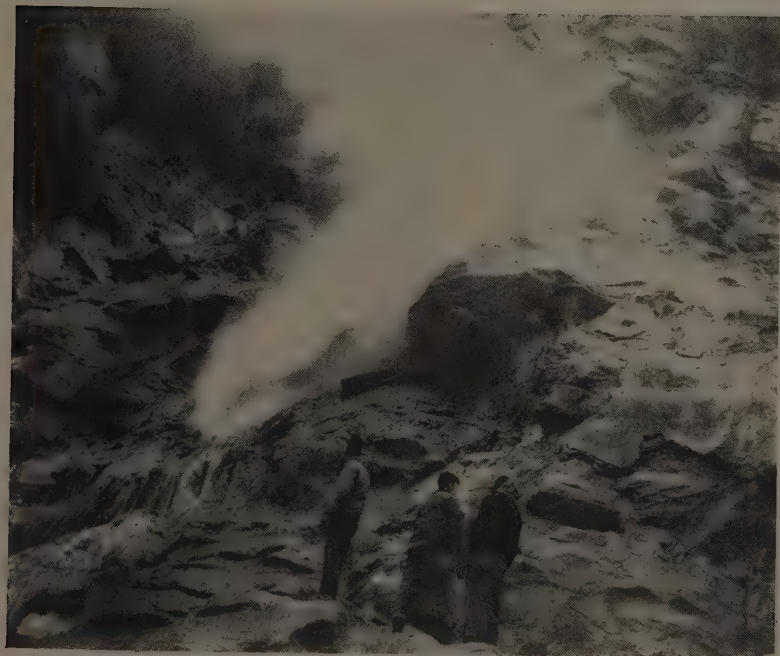


FIG. 2. Active steam jet near the sea, Kagamil Island, 1949

NATURAL REVEGETATION OF CERTAIN AREAS IN NORTHERN LOWER MICHIGAN FORMERLY COVERED BY BUILDINGS*

FRANK C. GATES

THE transfer of the University of Michigan Biological Station in Cheboygan County from the southeast side of Douglas Lake to the south shore of North Fishtail Bay in the winter of 1929-30 uncovered the sandy sites occupied by various buildings at the original location. Of the several available situations three were chosen to be set aside and fenced as preserves for subsequent study. They were sites that had been covered for short, medium, and long periods, as follows: the Research laboratory, three years, 1927-29; the Botany laboratory, six years, 1924-29; and the Houghton laboratory, sixteen years, 1914-29.

Both old and new sites are on soil designated as Eastport sand. It is a sand which had been developed and worked over when Douglas Lake was at a higher level. It has been exposed ever since the lake assumed its present level after the melting of the ice sheet. It is a rather sterile type of sand in which such plants as pines and blueberries grow but slowly. Being close to the level of Douglas Lake, it has a rather high water table which, however, is often disjunct from the surface. At the time of settlement the whole area was covered with pine. Logging, burning, and revegetation with the aspen association had taken place before the establishment of the Biological Station. A few seeding pines remained, however, and seedlings of pines were present here and there.

Each of the buildings was sledged bodily from its location to a center line and hauled away; thus no haulage occurred over any of the sites chosen for observation. All debris was cleared up during the winter of moving. On July 14, 1930, the areas chosen were fenced in and small creosoted stakes were put in to aid in mapping. Pictures have been taken in most of the summers since, and maps

* Contribution No. 514 from Department of Botany, Kansas State College, and a contribution from the Biological Station of the University of Michigan.

were made of the vegetation. We shall discuss the areas in turn, commencing with the one covered the shortest time.

THE RESEARCH LABORATORY SITE

The aspen trees on this area were cut early in 1927 and the sprouts mowed before the laboratory was built in the summer. The area covered contained about thirty-eight square meters. At the beginning of the summer of 1930 the outline of the laboratory was clearly marked on the ground (Pl. I, Fig. 1). During that summer the area became largely weed-covered, with an abundant influx of *Agropyron repens* from nearby grassy areas. Sprouts of *Populus grandidentata* and *Rhus glabra borealis* appeared and grew to a height of approximately a meter. Most of the twenty-four plants that appeared were annuals, largely of a weedy nature. Rosettes of *Verbascum thapsus* were present in greater numbers than any other species. In subsequent years aspens (*Populus grandidentata*) developed vigorously, reaching the largest number of shoots in 1933, after which through shading and competition the number was reduced to seventeen in 1939, thirteen in 1945, and seven in 1950. The increasing shade cast by an oak tree immediately outside the north boundary played a part in eliminating some of the aspens.

After five years of revegetation, controlled only by nature, the annuals were gone, except for one small plant of *Chenopodium album*, while the grasses and forbs which one associates with the aspens were present in such numbers and arrangement that, had one removed the fence, he would not have been able to outline the building. *Agropyron repens* and *Poa pratensis* were the main grasses to appear promptly. *Agropyron* spread in from the periphery by means of rhizomes, steadily becoming more abundant through 1935, after which it has been considerably thinned in the increasing shade. *Poa*, seeding in, reached its maximum in 1936. *Danthonia spicata*, *Poa compressa*, and *Panicum meridionale*, all normal to the aspens, have increased in number slightly as the years have passed.

Among the normal aspen forbs *Aster laevis* was present the first and second years, disappeared for two years, and since has been present in small numbers through the drouthy thirties. It has now increased to twenty-four plants. *Solidago hispida* appeared in 1933 as a single plant and barely maintained itself until the late forties.

It now has fifty-eight plants. The fern *Pteridium latiusculum*, so common in the aspens, represented by a single leaf the first year, made no showing until after the drouth. In 1950 thirty-one leaves were present. *Vaccinium angustifolium nigrum* first entered the area in the fourth summer and has increased but slightly. *Arctostaphylos waursi* appeared in the nineteenth year. Although an acorn-bearing oak (*Quercus borealis*) was just outside the area, no seedlings appeared until the fifth year, when forty-two were present. Many died. The number varied from year to year from a low of twenty-two in 1937 to a high of eighty-four in 1939 and 1940 (Pl. I, Fig. 2). Each year most of them die, but new ones come up. Very few are as much as five years old. *Acer rubrum* seedlings came in 1948, the nineteenth year. Nine are now present.

Pine cones were noted on the ground as early as 1933, but the first seedling to appear came in 1943 and a second in 1944. Both were growing slowly in 1950 (Pl. I, Fig. 3).

Mosses first appeared visibly in 1937, when *Ceratodon purpureus* invaded very sparingly in certain more open places. Moss has not made much progress in this area because of the excessive and nearly complete shade.

It has taken only five years to make up for the three years that plants were prevented from developing because of the presence of the building (Fig. 1).

THE BOTANY LABORATORY SITE

The Botany laboratory was built in 1924 in more open aspens, through the east half of which a sand road had been in existence for many years. The laboratory occupied about thirty-eight square meters of ground for six years before its removal. In the first summer after removal eighteen species made their appearance, all in modest quantities and most as single occurrences (Pl. II, Fig. 4). In subsequent years the number of species dwindled to eleven in 1938, since which time it rose slowly to nineteen in 1950. Aspens have not yet been an important element in the revegetation. Only since 1934, the fifth year, has any been permanent. There are now four, one of which is about 2 m. tall. Together they cast about one fifth as much shade on the area as a large aspen outside the tract to the south. All are *Populus grandidentata*. Moss, however, has

ABBREVIATIONS AND SYMBOLS USED IN FIGURES 1-4

Meter distances are marked along the edges of each plot.

Abbreviations of Specific Names			
A	Agropyron repens	PT	Pteridium latiusculum
AC	Acer rubrum seedlings	Q	Quercus borealis
AG	Agrostis alba	R	Rhus glabra borealis
AM	Amelanchier sp.	RO	Rosa (blanda)
AR	Arabis lyrata	S	Solidago hispida
AS	Aster laevis	SE	Setaria viridis
ASC	Asclepias syriaca	SJ	Solidago juncea
AU	Arctostaphylos uvaursi	V	Verbascum thapsus
CB	Carex bebbii	VA	Vaccinium pennsylvanicum ni- grum
CG	Carex gracillima	VI	Vitis vulpina
CH	Chenopodium album	Other Abbreviations	
CHR	Chrysanthemum leucanthemum	CON	Concrete footing not removed (Figs. 3 and 4)
CI	Cirsium pitcheri	LVS	Leaves
CO	Comandra umbellata	O	Open ground, i.e. without plants
CU	Carex umbellata	SP	Sparse
D	Danthonia spicata	ST	Stump
EA	Erigeron annuus	Numbers	
EC	Erigeron canadensis	Numbers immediately before letters des- ignating species indicate the number of plants found at the places indicated	
EL	Elymus canadensis	Numbers not immediately before letters:	
F	Festuca ovina	2 Very open sod	
G	Geaster hydrometricus	5 Open sod	
H	Hieracium aurantiacum	7 Dense sod	
K	Krigia virginica	Symbols	
L	Lepidium virginicum	● Populus grandidentata (Figs. 1 and 2)	
M	Ceratodon purpureus	● Populus tremuloides (Figs. 3 and 4)	
MP	Polytrichum juniperinum	≡ Areas covered with dead leaves	
OE	Oenothera muricata	\\ Areas shaded at noon	
PC	Poa compressa	/// Areas of moss cover	
PM	Panicum meridionale		
PP	Poa pratensis		
PRP	Prunus pennsylvanica		
PRV	Prunus virginiana		



FIG. 2. Revegetation on the Botany laboratory site in 1931 (left), in 1940 (center), and in 1950 (right)

(Pl. II, Fig. 6). The part of the area that had been a sandy road was the last part to become moss-covered. *Polytrichum juniperinum* first appeared in 1942 in small quantity in the masses of *Ceratodon* near the southwest corner and in the center of the south side.

Though this magnificent increase in moss cover did not cut down the total flora, it did materially lessen the number of individual plants to the point where the area now appears to be largely a bed of moss. The interstices are occupied by grass clumps rather than by sod grasses. *Danthonia spicata* was more common at first, but *Festuca ovina* increased much faster. Seedlings of *Rhus glabra borealis* appeared now and then, but only recently have they persisted. *Prunus pennsylvanica* does not establish itself. As the aspens in the area and those next to it grow larger and cast more shade, diminution of the moss carpet is to be expected, but meantime invasion of likely plants is greatly reduced.

Seeds of various plants studied in the laboratory dropped through the cracks in the floor. Some few grew in the first or the second season, such as *Chenopodium album*, *Epilobium angustifolium*, *Malva rotundifolia*, *Polygonum convolvulus*, *Polygonum persicaria*, *Rorippa hispida*, *Setaria viridis*, *Triticum aestivum*, and *Verbascum thapsus*. Most interesting of all, however, was the appearance the first year of a seedling of *Carex*, which the next year turned out to be *Carex gracillima*, a species normal to cedar bogs, here growing in open sand, wet season or dry season, very much out of habitat. Nevertheless it has persisted to the present time.

After the twenty-one years since this preserve was set up, it is still obvious just where the laboratory stood. As the shade of adjacent aspens and the few in the preserve gets denser, the area should become more and more an aspen area, as it had been (Fig. 2).

THE HOUGHTON LABORATORY SITE

Houghton laboratory was built in 1914 and covered about ninety square meters of ground for sixteen years. It was built on low pillars, so that the floor was not in contact with the sand. However, the edge of the building reached to the sand and thus shut off the light and prevented the development of plants underneath the building. With the removal of the building twelve species made their way into

TABLE I
INVASION OF PLANTS ON THE SITE OCCUPIED BY THE HOUGHTON LABORATORY DURING 1914-29
(The plus sign means "several"; the asterisk, "many.")

Species	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1942	1945	1949	1950
<i>Blitum capitatum</i>	2	1	1	..	..	..	..	..	..	..	..	..	..	..	..
<i>Cirsium pitcheri</i>	1	1	1	..	..	..	..	..	..	..	..	..	..	..	..
<i>Chenopodium album</i>	3	3	1	..	..	..	..	..	..	..	..	..	..	..	..
<i>Elymus canadensis</i>	2	+	+	+	5	9	8	5	7	6	8	..	3	2	..
<i>Galeopsis tetrahit</i>	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Lepidium virginicum</i>	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Oenothera muricata</i>	3	..	..	..	..	..	..	..	..	..	1	5	12	10	5
<i>Poa compressa</i>	+	+	*	+	+	+	*	+	+	+	+	+	*	*	*
<i>Poa pratensis</i>	+	+	*	+	+	*	*	*	*	*	*	*	*	*	*
<i>Populus tremuloides</i>	+	+	*	*	*	*	*	*	*	*	*	*	*	*	*
<i>Rumex acetosella</i>	1	..	..	..	..	..	..	..	..	..	..	4	29	25	26
<i>Trifolium pratense</i>	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
<i>Agropyron repens</i>	..	*	**	**	**	**	**	*	*	+	+	+	+	+	+
<i>Agrostis alba</i>	..	1	1	3	..	..	..	..	..	..	..	..	..	..	..
<i>Rhus glabra borealis</i>	..	1	1	1	2	7	14	9	6	6	9	9	4	1	1
<i>Rosa (blanda)</i>	..	4	..	..	1	1	1	2	2	1	2	2	2	2	3
<i>Arabis lyrata</i>	..	..	1	1	..	..	..	..	..	..	3	3	30	4	66
<i>Arabis (glabra)</i>	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..
<i>Prunus virginiana</i>	..	..	..	..	..	2	2	2	2	2	2	3	4	3	4
<i>Quercus borealis</i>	..	..	..	..	..	2	2	2	2	7	11	74	52	45	47
<i>Agropyron dasystachyum</i> ..	..	..	..	..	..	..	2	1	8	..	..	(also 1948)	6	4	6
<i>Amelanchier sp.?</i>	..	..	..	..	..	..	..	..	3	..	3	5	6	4	..
<i>Asclepias syriaca</i>	..	..	..	..	..	..	..	..	..	..	1	5	8	5	10

TABLE I (Concluded)

Species	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1942	1945	1949	1950
<i>Acer rubrum</i>	..	..	..	..	..	..	..	..	..	..	..	1	2	2	1
<i>Erigeron canadensis</i>	..	..	..	..	..	..	..	..	..	..	..	4	..	..	..
<i>Ceratodon purpureus</i>	..	..	..	..	..	..	..	..	..	..	..	+	+	+	+
<i>Asclepias phytolaccoides</i>	..	..	..	..	..	..	..	..	..	..	..	..	2	..	..
<i>Rorippa</i> sp.	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..
<i>Pteridium latiusculum</i>	..	..	..	..	..	..	..	..	..	..	..	..	5	..	8
<i>Solidago hispida</i>	..	..	..	..	..	..	..	..	..	..	(in 1948, 1)	1	1	1	1
<i>Prunus pennsylvanica</i>	..	..	..	..	..	..	..	..	..	..	(in 1948, 1)	..	..	..	4
<i>Polytrichum juniperinum</i>	..	..	..	..	..	..	..	..	..	..	..	..	..	..	+
	12	10	10	8	8	8	9	9	10	9	13	16	18	17	18

the area uncovered the first year, including at least five whose seeds probably came from activities in connection with the pressing of plants at the end of the building (Pl. III, Fig. 7). This area has been the slowest in revegetating, but has shown two lines of development. The earliest involved the spreading in from adjacent sand ridges of *Agropyron repens*, which came in the second summer and increased in density from year to year up through 1936 (seventh season), after which it decreased in density, although spreading in area somewhat. *Elymus canadensis* entered as two clumps in the first summer and increased during the next three years, since which time it has maintained a level of six to eight clumps. On the other hand, the sod grasses, *Poa compressa* and *Poa pratensis*, invaded promptly and increased year by year, reaching a maximum about 1938, but since then the accumulation of dead leaves has been instrumental in checking their normal extension.

At the west edge of the area aspens, here the tree *Populus tremuloides*, sprouted from the roots. The number of sprouts increased to a maximum in 1936, after which, although the number of stems diminished, the shade cast increased (Pl. III, Fig. 8). In 1950 there were twenty-six stems of *Populus tremuloides*, and 44 per cent of the area was shaded at noon. Two oak seedlings appeared in 1936, the seventh season. The number remained small through the drouth, but when wetter seasons came, the number reached seventy-four in 1942. At present (1950) it is forty-seven. Few of them live for more than a year or two. One *Acer rubrum* seedling appeared in 1942, a second in 1945, but only one poor plant remained in 1950. The common bracken fern, *Pteridium latiusculum*, although in the vicinity all the time, did not send rhizomes into the area until very late. Five leaves appeared in 1945, fourteen in 1949, and eight only in 1950 (Pl. III, Fig. 9).

Mosses first appeared in 1942, the thirteenth season, and have since increased in quantity, but are still very spotty in distribution, being kept in check by accumulations of dead leaves and increasing shade. The major species is *Ceratodon purpureus*, into whose areas a little *Polytrichum juniperinum* is now making headway.

This area, covered for sixteen years, shows by far the most open sandy appearance of all the areas. The revegetation had proceeded in greatest measure from the edges inward, instead of appearing all

over the area. The number of species is small; the twelve found in the first season dwindled to eight by the fourth season. With the

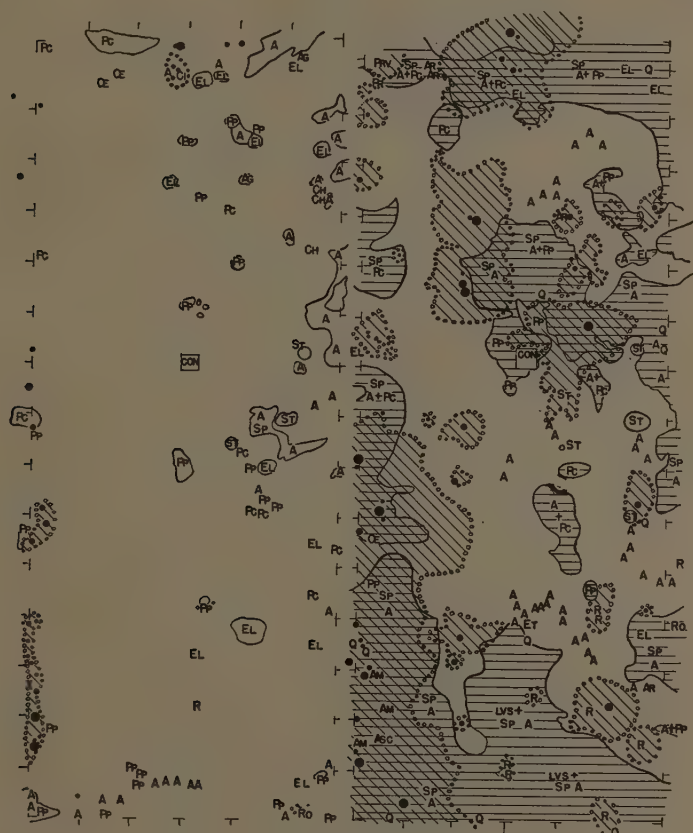


FIG. 3. Revegetation on the Houghton laboratory site in 1931 (left) and in 1940 (right)

close of the drouth of the thirties the number had risen only to seventeen in 1950. The species growing in this area are shown in Table I and in Figures 3 and 4.

NUMBER OF SPECIES IN REVEGETATION

Areas of this size in the aspen association usually have between twenty and forty species of higher plants. Reference to Table II will show the number of species that have been present in the revegetation of these areas in the various years as indicated. The area covered for the fewest years witnessed the greatest number of invaders the summer after uncovering and has maintained a more varied flora ever since. The early development of trees furnished shade and kept the grass element from closing over the land with sod. It also prevented the moss, *Ceratodon purpureus*, from being an important factor in revegetation.

TABLE II

NUMBER OF SPECIES IN REVEGETATION OF SITES

(The figures give the number of species present in the years indicated.)

Years covered	Laboratory site	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1942	1945	1948	1949	1950
3	Research	24	22	14	16	17	18	18	19*	18*	23*	22*	20*	24*	20*	22*	28†
6	Botany	18	14	14	14	12*	13	14*	12*	10*	12*	12*	16*	16*	17*	14*	18†
16	Houghton	12	10	10	8	8	8	9	9	10	9	13	15*	17*	16*	16*	16†

* The asterisk indicates that the moss *Ceratodon purpureus* is also present.

† The dagger indicates that both *Ceratodon purpureus* and *Polytrichum juniperinum* are present.

The site of the Botany laboratory, covered for six years, was invaded by only three fourths as many species the first year, although there were a number of additional species in the immediate vicinity. Tree species were very slow in invading, and consequently the shade factor was minor during the twenty-one years. Until recent years nearly all the shade in the area was furnished by trees outside—never sufficient to be an important factor. The moss *Ceratodon* took advantage of this, even in the drouth years. With wetter summers this moss spread rapidly and eliminated many individual plants of several species, although it did not seem to cut down the total number of species in the area. The contrast between this area and that covered by the Research laboratory is very great.

The site of the Houghton laboratory, covered for sixteen years, has been by far the slowest in its revegetation. Only a dozen species

invaded it in the first summer, and four of these did not last into the fourth year. At first shade was from the edges, but it did not become important until after a dozen years had passed. Sod-forming grasses came in from the sides also, but were not very successful against the dead weight of leaves which accumulated and smothered them. Shade, accumulated dead leaves, and a little blowing sand relegated mosses to an unimportant role in the revegetation of this area. In a special plot not far away, but quite similar, spores of *Ceratodon* were sowed. In the five years that have since elapsed there has been no sign of moss plants. There is still more open sand in this area than in both of the others together. It is evident,

TABLE III
DISTRIBUTION OF SPECIES BY AREAS

Species in only one area			Species in two areas			Species in all three areas
Research	Botany	Houghton	Research Botany	Research Houghton	Botany Houghton	Research Botany Houghton
25 56%	11 24%	9 20%	10 59%	5 29%	2 12%	16 100%
45 58%			17 22%			16 20%

78

however, that the effects of sixteen years' coverage are being overcome and that within another six or ten years the location of the laboratory will not be discernible to one who was not acquainted with the area in years past.

As will be seen from Table III, of the seventy-eight species concerned in the revegetation of these three areas forty-five, or 58 per cent, occurred in only one. Most of these were in the Research area, the area covered over the shortest time, to which twenty-five species, or 56 per cent, were limited. Sixteen, or 20 per cent of the seventy-eight species, were found in all three areas. Of these, thirteen, and probably fifteen, are typical plants of the aspen association. Only eleven of the species should be regarded as most unusual, and

nine can easily be explained as having come from seeds that fell through the cracks in the floor to the sand below, one from the feed of the horses used in moving the buildings, and the eleventh from bird seed carried to experimental duck pens.

SUMMARY

Areas covered over by buildings at the Biological Station of the University of Michigan for various periods of time have demonstrated that the longer an area is covered, the slower will be the natural revegetation, or, conversely, the shorter the time of coverage, the more quickly will the area be restored naturally to the appearance of the surroundings. Invasion of moss prolongs the restoration period.

KANSAS STATE COLLEGE
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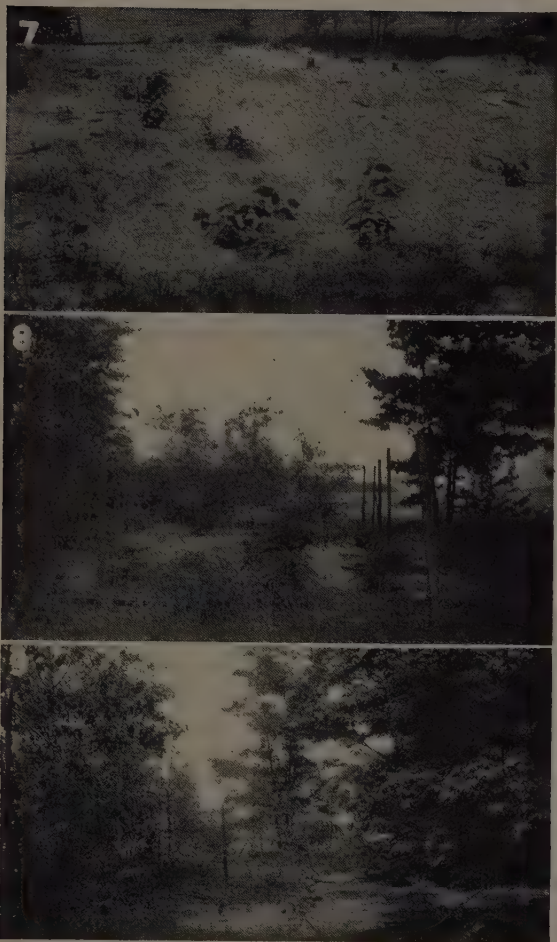
PLATES I-III



The Research laboratory site in 1930 (Fig. 1), 1940 (Fig. 2), and 1950 (Fig. 3)



The Botany laboratory site in 1930 (Fig. 4), 1940 (Fig. 5), and 1950 (Fig. 6)



The Houghton laboratory site in 1930 (Fig. 7), 1940 (Fig. 8), and 1950 (Fig. 9)

A NEW STREPTOMYCES THAT PRODUCES VITAMIN B₁₂ ACTIVELY

KENNETH L. JONES

IT IS now well known that vitamin B₁₂ is produced by many soil microbes and that from them it is apparently absorbed by higher plants, which in turn supply it to animals. Since the commercial production of this important vitamin is feasible by mass-culturing of *Streptomyces*, the chain may be shortened by adding to animal feed crude vitamin preparations thus obtained. The new species here described, *Streptomyces vinaceus* (Jones), has proved to be useful in this regard.

Morphology.—Spore-bearing, aerial hyphae straight, monopodially branched and never producing regular spirals. Conidiophores irregularly septate with branches at the septa. Conidia spherical, oval, or even cubical, with a diameter of 0.4 to 1.0 micron, usually about 0.7. Length of the oval or cubical spores up to twice their diameter. Conidiophores slightly wider than the spores and much coarser than the substratal hyphae.

Gelatin stab.—No liquefaction. A buff-gray colony, 5 mm. in diameter, forms on the surface of the gelatin. It has a lobed margin and an irregularly folded surface. A thin layer of aerial hyphae develops over most of the colony. An extremely slight growth occurs along the line of inoculation. A dark-brown pigment diffuses throughout the upper half of the medium.

Gelatin plates.—No liquefaction. Colonies like those on stabs, but up to 12 mm. in diameter and oval. As with the stabs, they become sunken deeply below the original level of the medium and produce deep pits. A dark-brown ring of diffusible pigment 5 mm. wide surrounds each colony.

Plain agar plates.—Substratal mycelium forms a barely visible, colorless, effuse growth. Colonies 17 to 26 mm. in diameter, margin lacerate. No diffusible pigment. Aerial hyphae scanty and white.

Nutrient agar plates.—Colonies oval, about 11 by 15 mm. Substratal mycelium as viewed from lower surface, chamois¹ in color,

¹ The color terms are those of R. Ridgway, *Color Standards and Color Nomenclature* (Washington, D.C., 1912).

becoming cream buff at the periphery; the upper surface dark olive buff, fading to pale olive buff at the margin. Aerial hyphae occupy central portion of colony and are white to pale vinaceous fawn. No diffusible pigment.

Starch agar plates.—Colonies circular, 18 to 23 mm. in diameter. Substratal mycelium as seen from lower surface vinaceous buff to tilleul buff. Upper surface covered with aerial hyphae colored light vinaceous fawn, with numerous white sectors in every colony. No diffusible pigment. Starch digested in zones 5 to 8 mm. wide around each colony.

Calcium malate agar plates.—Colonies oval, usually about 10 by 15 mm. Substratal mycelium, as seen from lower surface, vinaceous buff, fading to colorless at periphery. Aerial hyphae on central 5 mm. area light vinaceous fawn. Remainder of upper surface cream color to colorless. No diffusible pigment. Calcium malate digested in a zone 0.5 to 4 mm. wide around each colony.

Bennett's agar plates.—Colonies oval, usually about 20 by 25 mm. Substratal mycelium as seen from lower surface russet or chestnut brown, center with irregular patches or concentric rings of lighter brown, the periphery a cinnamon buff. Sporogenous hyphae vinaceous fawn to Army brown, practically covering surface of colony. Diffusible pigment of cinnamon-buff color.

Potato plug.—Thick, finely wrinkled growth of substratal mycelium over the entire surface. This growth is cream-colored at the base of the slant but becomes brown and finally black in the upper portion. Aerial hyphae absent or barely visible; white. The potato is darkened in the upper portion of the plug.

Nutrient broth.—A ring of growth 3 mm. wide forms at the surface on the wall of a flask or tube. This pulls away and, if it floats, forms sporogenous hyphae. The broth is clear, forms a coarse sediment, and becomes alkaline (pH 8.6).

Litmus milk.—Milk becomes alkaline (pH 8.7). Cartilaginous ring of growth on tube as for nutrient broth.

Dextrose, sucrose, lactose, maltose, and mannite.—Growth with alkaline condition developing. No gas.

Nitrate reduction.—Positive but not carried on strongly.

Source.—Isolated from soil collections.

Habitat.—Probably soil.

Note.—Produces vitamin B₁₂.

SOUTHERN AND TROPICAL POLYPORES*

JOSIAH L. LOWE

MANY of the polypores, in common with other fungi, occur over a very wide area. Additional collecting in hitherto inadequately explored regions supplements records within the known ranges, and occasionally markedly extends the known distribution of rare and endemic species.

Very few monographs on the family Polyporaceae cover wide areas. Lloyd (1905-25) has treated certain genera for the world; Pilát (1936-42) has published a comprehensive manual for Europe, and Murrill (1907-08, 1914, 1915 a, b, c) has described the North American species.

The polypore flora of the southeastern United States presents a fascinating opportunity. The flora is now reasonably well known, but the distribution records are very incomplete. Two important papers have recently been published on the species occurring in the lower Mississippi Valley (Overholts, 1938) and in Florida (Murrill, 1947). Over several years Baxter (1934-50) has added much information on the resupinate polypores. Numerous papers of lesser scope have also appeared.

The plants in southern Florida and southern Texas merge with subtropical and tropical floras, and a number of typically tropical polypores are known to occur in these states. New elements may be expected. Two species hitherto unreported from the United States are included in this paper, and other specimens at hand, as yet unidentified, will add to this list. Many tropical polypores are known to have world-wide distribution. Comprehensive study in the southern United States inevitably brings the tropical polypore flora of the world under survey. Elements of South American and East Indian floras are well known from the work of Lloyd and Murrill, and I (Lowe, 1947, 1948) have recently reported a few examples. The tropical representatives in Central America and the West

* Contribution from the Department of Forest Botany and Pathology, State University of New York, College of Forestry, Syracuse, New York.

Indies are in need of critical study, and, particularly, the species described from tropical America need to be compared with the rich polypore flora of the East Indies.

The present paper, which is a report on collections of unusual interest made in the summers of 1949 and 1950,¹ records a marked extension of the known ranges of *Polyporus spathulatus*, *P. subcartilagineus*, and *P. tepeitensis*; it supplies additional taxonomic information on *Fomes taxodii*, *Polyporus fissilis*, and *P. floriformis*; and *Polyporus submurinus* is placed in synonymy with *P. meliae*.

Polyporus spathulatus (Hook.) Fries

This species is reported by Murrill (1915 b, p. 73) as frequent throughout tropical America. Although no collections in the United States have hitherto been reported or seen, numerous specimens were collected on the ground in early September, 1950, near Homestead, Florida. The fruiting body appears like small multiplex specimens of *Polyporus cinnamomeus* Jacq. ex Fries. The upper surface is a beautiful silky-yellowish brown, but the very minute pores, about 10–15 per mm., readily distinguish it from all other similar stipitate brown species, which have very much larger pores, 1–4 per mm.

The spores, not previously described, are brown, smooth, broadly ellipsoid, $2.5\text{--}3 \times 1.5\text{--}2 \mu$. The hyphae are abundantly septate as in *Polyporus cinnamomeus* and similar species, but narrower, 3–4 μ , rarely 5 μ , in contrast to a diameter of 4–7 μ in all the similar species.

Polyporus subcartilagineus Overh.

Only three collections of this species have been reported, two from Quebec and one from Pennsylvania. The species is, however, rather common in the Adirondack Mountains of New York, and is also common in the high-mountain country of western North Carolina and the Great Smoky Mountains of eastern Tennessee. It has been and very readily is confused with *Polyporus fragilis* Fries. In the fresh condition the context tissue next to the substratum is translucent and rather crisp (not watery); this is a good field characteristic. Certain distinction, however, turns upon differences in the

¹ In 1950 I was in the employ of the Division of Forest Pathology, Bureau of Plant Industry, Soils and Agricultural Engineering, United States Department of Agriculture.

spore shape. In *P. subcartilagineus* the spores are short-cylindric, $4.5-6.5 \times 2-3 \mu$; in *P. fragilis* they are slender, allantoid, $4-5 \times 1-1.5 \mu$.

The rot associated with *P. subcartilagineus* is of the brown cubical type.

***Polyporus tepeitensis* (Murr.) Lowe, comb. nov.**

This species was described (Murrill, 1912, p. 142) from three collections made near Cuernavaca, Mexico. No additional collections appear to have been made until very recently, when abundant material was found on sassafras, black locust, and sumach near Gatlinburg, Tennessee, in the Great Smoky Mountains National Park, always on standing small trunks or limbs some distance above the ground.

Some distinctive features of this plant are not included in the original description. The hyphae are nonseptate, solid, $1.5-2.5 \mu$ in diameter, and the spores are hyaline, smooth, broadly oval, $5-6 \times 5 \mu$. These microscopic characters readily separate the species from immature specimens of other species of similar external appearance, for example, *Polyporus ectypus* Berk. & Curt., *P. hollickii* (Murr.) Lloyd, *P. semisupinus* Berk. & Curt., and *P. subectypus* (Murr.) Bres.

***Fomes taxodii* Murr.**

This species, described from sterile material collected on *Taxodium* in northern Florida, was found rather frequently in fertile condition on the same host in the Okefenokee Swamp in Georgia in 1950. The spores are hyaline, smooth, broadly ellipsoid, $4.5-5 \times 2.5-3 \mu$. Type material, kindly loaned by Dr. W. A. Murrill, had setae, as did my own collections, although they were said to be absent in the original description (Murrill, 1938, p. 651). The setae are subulate, $20-30 \times 6 \mu$.

***Polyporus fissilis* Berk. & Curt.**

This species frequently occurs in a nodular condition in Georgia and northern Florida and is then indistinguishable in the field from *Polyporus compactus* Overh. The chlamydospores afford ready separation. In *P. fissilis* they are ovoid, $5-7 \times 3-5 \mu$; in *P. compactus* they are larger, $8-11 \times 7-9 \mu$.

Polyporus floriformis Quél.

A collection (Lowe, 4483) made in western North Carolina on *Liriodendron* appears to be the second report of this species on a hardwood substratum. Zeller (1922, p. 182) has previously reported it on maple from Oregon.

Polyporus meliae Underwood

The type of this species is represented by two specimens in excellent condition, both with the annual growth typical of the genus *Polyporus*. The species was transferred to the genus *Fomes* by Murrill (1903, p. 232) for reasons not now apparent, as there are no specimens in the New York Botanical Garden that support the transfer, and no such material has been seen elsewhere. Occasionally, as in several other species of *Polyporus*, the fruiting body may revive and form a second, poorly developed, layer of tubes.

Its supposed perennial nature has, among other characteristics, served to separate this species from *Polyporus submurinus* (Murr.) Lloyd. On direct comparison of the type material of both species it became clear that the growth habits of the two differ somewhat, but the internal microscopic details, in particular the hyphae and the hymenial elements, agree exactly. *Polyporus submurinus*, therefore, should be relegated to synonymy under the earlier valid name, *P. meliae*.

Lloyd (1905-25, 4: 283) believed that this species was synonymous with *Fomes connatus* (Weinm.) Gill. Externally the type of *Polyporus meliae* closely resembles the first year's growth of *F. connatus*, but internally the two species are entirely dissimilar.

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STUDIES IN PLANT CARBONIC ANHYDRASE*

I. OCCURRENCE, DISTRIBUTION, AND PROPERTIES

EUGENE H. LUCAS AND RICHARD U. BYERRUM

AT THE annual meeting of the Michigan Academy of Science, Arts, and Letters in 1948 the senior author presented a paper entitled "Preliminary Report on Carbonic Anhydrase in Plants." It recorded the occurrence of carbonic anhydrase in the leaves of more than thirty species of phanerogams. At that time the senior author was unaware of a paper by Bradfield (3), published in 1947, which essentially had shown what the preliminary report was supposed to show, namely, the wide occurrence of carbonic anhydrase in leaves of green plants. Until Bradfield's paper appeared several contradictory statements had been published on this subject (2, 3, 5, 6). The senior author's paper thus confirmed Bradfield's finding that carbonic anhydrase could be generally detected in photosynthetic tissue provided adequate techniques were employed.

Shortly before the present material was assembled an extensive study was published by Waygood and Clendenning (7) which in many respects coincides with the subject of this paper. Apparently work on plant carbonic anhydrase was conducted independently by both the Canadian group and the Michigan State College group at the same time. The main results and conclusions are in agreement.

OCCURRENCE IN PLANTS

It can now be assumed that the existence in the leaves of green plants of an enzyme which catalyzes the reversible reaction $\text{CO}_2 + \text{H}_2\text{O} \rightleftharpoons \text{H}_2\text{CO}_3$ is an established fact. The main incentive for a search for plant carbonic anhydrase has been its possible connection with photosynthesis. This possibility was first suggested by Burr (2), but was ruled out on the basis of experimental evidence and theoretical considerations. The results obtained by several investigators (1, 3, 6, 7) have shown a rather wide range of activity. Although each

* Journal Article No. 1211 of the Michigan Agricultural Experiment Station. Part II will appear in *Plant Physiology*.

worker or group of workers has used a different way of expressing enzyme activity, it has become apparent that there are some plants with high activity and others with very low activity. Several environmental factors, however, play a role in the enzyme activity measured under various conditions. Waygood and Clendenning (7, 8) express enzyme activity in a manner similar to that of Meldrum

TABLE I
PLANT CARBONIC ANHYDRASE ACTIVITY IN LEAF EXTRACTS OF SOME SPECIES
OF PLANTS
(e. u. = enzyme units)

High activity (over 80 e. u.)	Medium activity (between 20 and 80 e. u.)	Low activity (below 20 e. u.)
Species		
Tulipa Gesneriana	Medicago sativa	Triticum vulgare
Polygonum persicaria	Cucumis sativus	Rumex crispus
Rubus strigosus	Phaseolus vulgaris	Arachis hypogaea
Raphanus sativus	Antirrhinum majus	Daucus carota
Capsicum annuum	Chrysanthemum hortorum	Matthiola incana
Chenopodium album	Dianthus caryophyllus	Hydrangea paniculata
Brassica oleracea		Vinca minor
Pisum sativum		Lycopersicon esculentum
Lathyrus odoratus		Cyclamen persicum
Phaseolus lunatus		Allium cepa
Gypsophila paniculata		Cytisus genista
Lupinus angustifolius		Urtica dioica

and Roughton (4) in their pioneering work on animal carbonic anhydrase. An enzyme unit is used which is derived from the ratio $\frac{R-R_o}{R_o}$, where R equals the rate of catalyzed dehydration and R_o equals the rate of uncatalyzed dehydration in a given time. In earlier work the authors also used this ratio. It was soon found, however, that for comparative measurements the ratio is inadequate. Meldrum and Roughton dealt with a single material, blood, whose composition was very uniform. Plant extracts vary considerably in dry matter, and it was therefore considered necessary that the ratio express this variation. For this reason the ratio $\frac{R-R_o}{g}$, in which g equals weight in grams of dry matter, was substituted.

Table I compares the activities of a number of species tested. In order to take into consideration variations owing to environmental conditions the results were summarized after at least ten tests of each species at different times of the year, under different growing conditions and at different ages. These tests have given occasional overlapping of enzyme values, and it was therefore thought advisable to arrange the species in three groups, representing high, medium, and low enzyme activities. In each case the activity was determined manometrically. The shaking of the enzyme solution and substrate took place in a water bath of 30° C. The shaking unit was fitted with

TABLE II
COMPARISON OF CARBONIC ANHYDRASE ACTIVITY IN LEAVES
AND OTHER GREEN PARTS OF PHASEOLUS VULGARIS AND
CHENOPODIUM ALBUM

Species	Leaves	Stems	Stems and petioles
	Enzyme units		
<i>Phaseolus vulgaris</i>	70	14	..
<i>Chenopodium album</i>	105	..	26

an Erlenmeyer flask with divided bottom. The rate of shaking was 120 oscillations per minute. Since mixing was found to be uniform from the outset of shaking with negligible variations, the measurements were started at zero time. Two milliliters of 0.2 M phosphate buffer of pH 6.8 and 2 milliliters of 0.1 M sodium carbonate in 0.01 M sodium hydroxide were used as substrate. One-half to one milliliter of enzyme solution was added, according to the concentration and activity of the material. The activity was determined by subtracting the uncatalyzed rate (boiled control) from the catalyzed rate and was expressed in micromoles, per gram of dry weight, of CO₂ evolved in thirty seconds. The values thus obtained are enzyme units (e. u.).

The enzyme seems to be present in all plant parts participating in photosynthesis. Internodes of kidney beans, and stems and petioles of lamb's-quarters were found to have definite, though low, activity (Table II).

It is interesting to note that low activity was also established in a species of *Euglena* grown in a rice-wheat medium. In most plants the older leaves have higher enzyme activity. Table III

shows that leaf age is not necessarily correlated with activity. While tulip leaves, for example, were less active when young, mature leaves of snapdragon were less active than young ones.

LOCALIZATION IN THE CELL

The work of Waygood and Clendenning (7, 8) has clarified the question of intracellular localization. They showed that a single high-speed centrifugation of the leaf extracts left only 2 to 50 per cent of the carbonic anhydrase activity in the chloroplast fraction. Washing with water removed an additional part of the activity from the chloroplasts (7).

TABLE III
PLANT CARBONIC ANHYDRASE ACTIVITY IN RELATION TO
AGE OF LEAVES

Species	Age of leaves	Enzyme units
Tulipa Gesneriana	Mature	104
	Young	48
Antirrhinum majus	Mature	26
	Young	40

These findings have been in general confirmed in the experiments of the authors. Since the first separations were performed by a method similar to that used by Meldrum and Roughton (4), this result was somewhat unexpected. Meldrum and Roughton, using ox-blood corpuscles as the source of enzyme, shook a water-ethanol suspension with chloroform and then centrifuged. They obtained a top layer of enzyme solution, a central layer of denatured protein, and a bottom layer of chloroform (4). When water extracts of leaves were subjected to a similar treatment, the main activity invariably resided in the supernatant liquid. A flocculate, which occasionally formed, and the chloroplast fraction showed considerable activity at first. This activity, however, was quickly lost on storage, whereas that of the supernatant remained stable for some time (Fig. 1).

PROTECTIVE AND INHIBITING PRINCIPLES

It was pointed out in the paper presented at the Academy meeting in 1948 that the apparent absence of the enzyme in certain plants

may be due to the inability to retain the activity in the extract. Any destructive agent which might come in contact with the enzyme

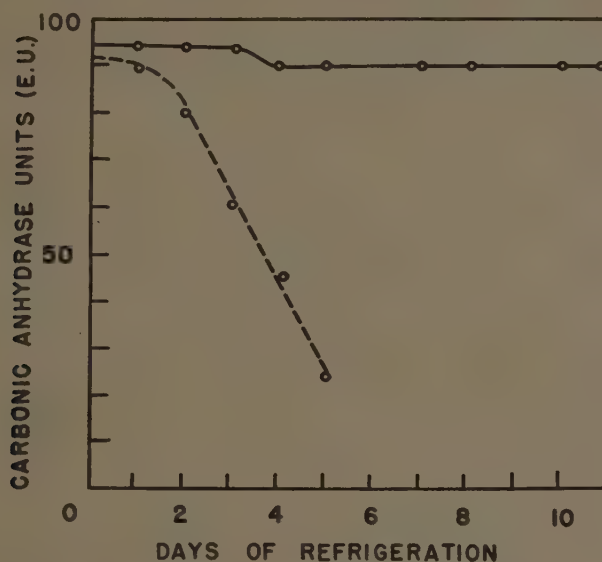


FIG. 1. The rate of degradation of carbonic anhydrase activity in the supernatant (solid line) and the chloroplast fraction (broken line) of centrifuged leaf extract of *Pisum sativum* held in a refrigerator

TABLE IV
THE RETENTION OF CATALYTIC ACTIVITY IN LEAF EXTRACTS
AFTER BOILING

Species	Fresh extract	Boiled extract
	Enzyme units	
<i>Tulipa Gesneriana</i>	115	15
<i>Pisum sativum</i>	96	7

during the process of maceration could be responsible for it. Waygood and Clendenning, who also investigated this possibility, did not find an inhibiting effect of tomato-leaf extracts, which have very low

enzyme activity, on parsley-leaf extracts when blended with them (7). As reported in 1948, tomato-leaf extracts showed an increase of activity when boiled pea-leaf extracts were used in their preparation instead of water. It was assumed then that a protective substance contained in the pea leaves but absent in tomato leaves might have been responsible for this phenomenon. In the light of the present studies it seems more likely that this effect is due to the weak activity

TABLE V
STABILITY OF CARBONIC ANHYDRASE IN PLANTS FROZEN AFTER HARVEST
AND STORED AT -5° F.

Species	Fresh leaves	Stored six months	Stored one year	Stored two years
	Enzyme units			
<i>Tulipa Gesneriana</i>	120	124	125	120
<i>Chenopodium album</i>	110	110	105	105

TABLE VI
STABILITY OF CARBONIC ANHYDRASE EXTRACTS AT 0° F.

Nature of extract	Freshly prepared	Stored for five months and thawed
	Enzyme units	
<i>Chenopodium album</i> leaves blended with three times their fresh weight of water	87	80

of a heat-stable catalyst in the pea leaves. It has been observed that the heated controls of some leaf extracts still retain weak activity (Table IV). For this reason boiled controls were used in most of the experiments instead of water controls in order to determine the enzyme activity.

STABILITY

In general, the enzyme activity has been found to diminish rapidly. Some leaf extracts, however, for instance, those from tulip and lamb's-quarters, retained activity over a remarkably long period.

Both materials were frozen and stored for periods of several months to two years at temperatures of 0° F. and below and did not lose much of their enzyme activity (Tables V and VI).

SUMMARY

1. The general occurrence in green tissues of phanerogams of an enzyme catalyzing the dehydration of carbonic acid is reported.
2. Similar enzyme activity could also be detected in the photosynthesizing protozoon *Euglena deses*.
3. Plant species have a well-defined level of activity ranging from high to very low.
4. The enzyme activity is located in the cytoplasm.
5. At temperatures below 0° F. enzyme activity is retained to a considerable extent in the plants as well as in extracts.

This work will be published elsewhere in greater detail.

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A PRELIMINARY ACCOUNT OF OENOTHERA TYPES IN THE KEWEENAW PENINSULA OF MICHIGAN

CHARLES D. RICHARDS

DURING the summers of 1949 and 1950 I critically botanized localities in the Keweenaw Peninsula of Michigan with the purpose of subjecting to a test M. L. Fernald's conclusion that that area was a refuge for plants during the last glacial period. Even if his hypothesis in unmodified form is not acceptable, there is at least a possibility that parts of the Keweenaw Peninsula sustained vegetation a considerable time before the general melting of the ice, and such a modification of the hypothesis might possibly explain some of the peculiarities of distribution of certain plants. In the course of the work special attention was directed to *Oenothera* because of the diversity shown by this remarkably variable genus.

In this paper there is no speculation about the relative antiquity of the various types that were found to be distinguishable. It is clear, however, that the localities of plants of disjunct distribution, like West Bluff, were not remarkable for diversity or unusual localization of their *Oenothera* flora.

I am not attaching names to the various distinguishable entities because, as this article is being written, it is reported that Professor R. E. Cleland has in press a book dealing with the *Oenothera* problem, and Professor R. R. Gates has a revision of this genus ready for publication. These works are expected to present much of the previous investigation in better perspective than does anything now in print.

It would needlessly complicate the situation to publish with names a detailed account of the distinguishable types of one small region. It will help to indicate roughly the characteristics by which the *Oenothera* population of a restricted area can be classified into entities that are genetically distinct. I have not tested these plants by garden cultures, but the distinctive traits are such as have been found by several workers to breed true with extraordinary constancy.

In keying out distinguishable entities I do not consider it necessary to go to the ultimate degree of subdividing, and at the moment I see no need for long descriptions. On the contrary, I present a key which in the main provides contrasting features that can be distinguished after one attains reasonable familiarity with the group. Types may be named later if they do not fall reasonably well into the categories provided in the forthcoming works of Cleland and Gates.

Since no names are here assigned, there is no need to worry about what represents a species, a variety, or a form in the Keweenaw flora. For the present it is sufficient to indicate that in two field seasons devoted no more intensively to *Oenothera* than to several other critical genera, twenty-one distinguishable entities turned up, and various others that were not in proper condition for study. The number is about what one would expect in view of earlier and almost entirely unpublished studies by H. H. Bartlett and others. These studies indicate that in any locality containing more than one genetic entity there will probably be four or more others, since the phenomena of twin hybrids and of mixed patrocliny and matrocliny are likely to give at least four types from each two distinct basic types. If a locality has more than six types, it is to be expected that some will not be distinguishable from the standpoint of practical systematic botany.

As for the method of attacking such a complicated problem, it is interesting to consider what each locality and habitat provides in the way of systematic entities that would unquestionably have nomenclatural status if they had any determinable geographic range. The distinguishing of genetic or, at least, systematically satisfactory types over a reasonable geographic range is now one of the greatest difficulties that confronts the botanist who is not willing to throw a medley of distinguishable genetic entities together under a single name that has no significance either geographically or biologically.

I have, therefore, made somewhat of a departure in *Oenothera* literature by keying out everything that I could from a geographically natural region, and then indicating the expectations for single localities and habitats.

The Keweenaw Peninsula, which is the geographical region under consideration, projects into Lake Superior in a northeasterly direction from the main part of the Northern Peninsula of Michigan. It is approximately 65 miles long, 28 miles wide at its southern end, and about 2.5 miles wide at its northern tip. Parts of three counties are

included within its boundaries, namely, Keweenaw, Houghton, and Baraga. Although much of the peninsula is forested and unsuited to maintaining populations of *Oenothera*, there are numerous places that offer excellent habitats for these plants, which prefer a disturbed soil. Such habitats are found on the sandy and gravelly beaches, on old mine sites, in abandoned quarries and fields, along roads and railroads, and around sawmills and lumbering camps. An attempt was made to visit as many of these kinds of localities as possible and to make critical collections from the *Oenothera* population present.

An enumeration of these localities follows, with a brief description of the habitats and of the *Oenothera* types found in each.

KEWEENAW COUNTY

1. *West Bluff*

West Bluff was made famous by Professor Fernald, who considered it a nunatak refuge for plants during the maximum Wisconsin glaciation. It extends in an east-west direction parallel to the shore of Lake Superior. At its highest point it rises 735 feet above the lake level. The north side of the bluff slopes gently toward Lake Superior and is covered chiefly by young aspen stands with many grassy openings. The south side of the bluff consists of deeply weathered trap and conglomerate cliffs with a well-developed talus slope, which merges into the forest of the valley. The rim of these cliffs, which is constantly being swept by a strong wind blowing up from the valley, consists of rotted conglomerate and presents a bleak habitat for plant life. Three collections of *Oenothera* were made on the barren summit of these cliffs. These were associated with species which Fernald considered preglacial relicts, namely, *Chamaerhodos Nuttallii* var. *keweenawensis*, *Ceanothus sanguineus*, *Carex Rossii*, *Woodsia oregana*, and *Potentilla pensylvanica*.

It is to be presumed that, if Fernald's hypothesis is true, any localized *Oenothera* might conceivably be added to the relict group, and particular attention was therefore given to securing representative material of whatever was there. It turned out that only one distinguishable type was present, which was not highly localized, being found at other localities which were never considered nunataks. Of course, since *Oenotherae* are of definitely weedy propensities, there is no reason why the range of nunatak relicts might not have become extended even somewhat erratically, since the forest was widely cleared.

The single *Oenothera* type, which was collected under numbers 1043, 2443, and 3789, has the following distinguishing characters: calyx tips subterminal; inflorescence declinate when young; ovary not conspicuously red-papillate; hypanthium yellow; ovary very densely and hypanthium densely viscid-pubescent, both also pilose but with no visible crispate short pubescence among the pili.

2. *Phoenix Mine*

This locality presented an artificial habitat on which the sampling of the *Oenothera* population indicated the presence of only one type. The abandoned copper mine produced a hilly gravel dump on which the vegetation was very meager, so that the soil was not fixed, and not many species are successful invaders. The single *Oenothera*, collected under number 2052, was somewhat depauperate but healthy, and belonged to the *litorea* assemblage. Its distinguishing characters are as follows: calyx tips subterminal; inflorescence declinate when young; ovary not conspicuously red-papillate, almost lacking viscid pubescence, but with dense crispate pubescence among the pili; hypanthium yellow, only moderately viscid-pubescent.

3. *Great Sand Bay*

This locality is about two miles east of the village of Eagle River. It is a broad bay with a pebbly beach and steep sand dunes behind the beach. An attempt has been made to arrest the shifting dunes by planting pines and beach grass. Conspicuous native pioneers on the dunes are *Lathyrus japonicus*, *Artemisia caudata*, and *Oenothera* sp. At this locality the constant shifting of surface soil, so conducive to the multiplication of *Oenotherae*, comes about from erosion and redeposition by wind.

The single *Oenothera* type was collected under numbers 2770 and 3806. It can be distinguished from other members of the group by the following characters: calyx tips subterminal; inflorescence declinate when young; ovary conspicuously red-papillate; hypanthium red. In the last characteristic it resembles *O. perangusta* var. *rubri-calyx*, recently described from the Thunder Bay District, Ontario, by Gates.¹ It differs from Gates's plant, however, in having the ovary conspicuously red-papillate.

¹ Gates, R. R., "Another Parallel Mutation in *Oenothera*," *The Canadian Field-Naturalist*, 64 (1950): 142-145.

4. *Eagle River*

This is a locality on the north shore of the Keweenaw Peninsula. Two collections of *Oenothera* were made here, which proved to be different. No. 4832 was growing on the sandy beach along Lake Superior and No. 4375 along the road at the edge of the village. Their distinguishing features are as follows: (1) 4832: calyx tips subterminal; inflorescence declinate when young; ovary not conspicuously red-papillate; hypanthium red. This may correspond to *O. perangusta* var. *rubricalyx* of Gates. (2) 4375: calyx tips subterminal, 0.5 to 1.0 mm. long; inflorescence not declinate when young; ovary not conspicuously red-papillate, densely gray-pubescent.

5. *Bete Gris Bay*

This large bay is located on the south side of the Keweenaw Peninsula near its tip. The beach is sandy and flat, and the dominant vegetation consists of red pine. On the open beach *Hudsonia tomentosa*, *Lathyrus japonicus*, *Prunus pumila*, and *Oenothera* sp. were among the most prominent plants. The *Oenothera* population appeared to be quite uniform, so that only a single collection was made, number 3684. Its distinguishing characters are: calyx tips subterminal; inflorescence declinate when young; ovary conspicuously red-papillate; hypanthium yellow; ridge at back of bract with red papillae extending onto it from stem ridge.

6. *Mandan*

This locality is a ghost town about five miles east of the present village of Delaware. The houses of the old mining town are still standing, but for many years the yards and gardens have yielded nothing except large crops of weeds. *Oenothera* has found a suitable habitat here, but diversity in the population is apparently not great, since only one distinguishable type was found. It is number 4431 and can be defined as follows: calyx tips terminal; ovary conspicuously red-papillate; bracts shorter than the buds; bud cone and hypanthium yellow.

This type was found at many other localities, and it is undoubtedly the most common one on the peninsula.

7. *Lake Upson*

This small lake is located at the western end of West Bluff, and the *Oenothera* population here consisted of several colonies along the road to the north of the lake. The single collection bears number 3797 and is not readily distinguishable from Mandan 4431.

8. *Fort Wilkins*

This old fort, now reconstructed and preserved in a state park, is located one mile east of Copper Harbor not far from the northern end of the peninsula. *Oenothera* is by no means a conspicuous element in the flora around the fort, but occasional plants were found in disturbed soil. A single collection, 2522, appeared to belong to the same type, which proved to be, for all practical purposes, identical with Mandan 4431.

HOUGHTON COUNTY

1. *Houghton*

Several collections of *Oenothera* were made in the vicinity of the village of Houghton, which is on the shore of Portage Lake. Two disturbed areas, namely, the railroad tracks in town and the roadside south of town, gave rise to fine populations of *Oenothera*. These two localities were man-made and consequently weedy, but there is no reason to suppose that the evening primroses were other than those naturally occurring in the locality. Four distinguishably different types were found in these localities: 4438a (railroad tracks): calyx tips subterminal; inflorescence not declinate when young; bracts with definite abscission zone. (2) 4440 (railroad tracks): calyx tips terminal, in mature buds 5 to 7 mm. long; ovary not conspicuously red-papillate; stem conspicuously red-papillate. (3) 4233 (roadside): calyx tips terminal; ovary not conspicuously red-papillate, densely gray-pubescent. (4) 4235 (roadside): same type as Mandan 4431.

2. *Lake Linden*

This locality was a roadside about a half mile east of Lake Linden. The *Oenotherae* were growing in a broad, shallow depression between the road and a fence enclosing a cultivated field. The plants were tall and vigorous, and several fasciated specimens were found among them. Here the evening primroses were definitely more abundant because of recent movement and disturbance of surface soil and

probably represented the types originally found in or near the locality before the soil surface had been disturbed by the grading of the road. Eight collections were obtained at this locality, all belonging to the same type as Mandan 4431. They were 3662, 3663, 3664, 3665, 3665a, 3666, 3667, 3669.

3. Dollar Bay

This is a small village about four miles east of Hancock. A considerable amount of waste ground along the railroad tracks afforded an excellent disturbed habitat for the multiplication of *Oenotherae*. Five rather distinct types were collected here: (1) 3866, 3868, 3878: same as Mandan 4431. (2) 3883: calyx tips terminal; ovary conspicuously red-papillate; hypanthium yellow; stem, ovary, bud cone, and hypanthium only moderately pilose. (3) 3870: calyx tips terminal, those of mature buds 2 to 4 mm.; ovary not conspicuously red-papillate; stem not red-papillate. (4) 3874: calyx tips terminal; ovary not conspicuously red-papillate; bud cone with 8 stripes of purple splotches. (5) 3876: same as Houghton 4233.

4. Otter Lake

This lake, which is about fourteen miles south of the village of Houghton, has stretches of gravelly shore dominated by willow. Between the water and the road *Oenothera* was well established in several places. It is difficult in such a locality to appraise the effect of soil disturbance during road building, but one may say with fair assurance that, if there was any disturbance, the effect would have been to increase the abundance of the local types even if no others happened to be brought in. There proved to be four distinguishable types in the six collections made at this locality. They are: (1) 3818, 3832, 3861: same as Mandan 4431. (2) 3579: calyx tips terminal; ovary conspicuously red-papillate; hypanthium yellow; buds shorter than bracts; back of bracts, hypanthium, and bud cone with some red papillae. (3) 3861a: calyx tips terminal; ovary conspicuously red-papillate; hypanthium yellow; bracts shorter than buds; some red mottling and red-based papillate hairs on bud cone. (4) 3861b: calyx tips terminal; ovary conspicuously red-papillate; hypanthium yellow; stem, ovary, bud cone, and hypanthium conspicuously pilose; bracts densely pilose on white nerves below, with subglabrous, wine-red areas between veins.

5. *Jacobsville Quarry*

Jacobsville is on the east side of Portage Entry. At one time the quarrying of red sandstone was an important industry here, but the quarry has been abandoned for many years and the bottom is becoming overgrown with vegetation. In this new habitat *Oenothera* is one of the conspicuous pioneering genera, and two distinguishable types were collected in it. They are: 3597: same as Bete Gris Bay 3684, 3602: calyx tips subterminal; inflorescence declinate when young; ovary conspicuously red-papillate; hypanthium yellow; ridge at back of bract with red papillae extending onto it from stem ridge.

6. *Big Traverse Bay*

This is a broad bay on the east side of the Keweenaw Peninsula, lying between Traverse Point and the village of Gay. The gently sloping beach is almost pure sand with sparse vegetation. An unsurfaced road extends parallel to the beach, and along this road *Oenothera* was common. Here grading for the road has undoubtedly disturbed the soil enough to account for the large *Oenothera* population, but there is no reason to regard the types as other than native to the locality. Two distinguishable types were found: (1) 3660: same as Bete Gris Bay 3684. (2) 3661: same as Mandan 4431.

7. *Bear Lake*

This locality is about ten miles north of the town of Hancock and about one-fourth mile inland from Lake Superior. Two collections of *Oenothera* were made on the shore of the lake and were given the numbers 1231 and 3999. The former agrees with the type already described as Mandan 4431, and the latter is similar to Dollar Bay 3870.

8. *Silver Mountain*

This locality is in Laird Township. Most of the mountain has been burned, exposing large surfaces of bare granite with beautiful glacial striations. The plant cover on this surface is rather sparse, but *Oenothera* is one of the plants that have become established. The single type, No. 2298, agreed in its characteristics with Mandan 4431.

9. *St. Louis Hill*

This locality is about two miles east of the town of Laurium. A large population of *Oenothera* was found growing along an unsurfaced road. A sampling showed it to be uniform and the type to be distinct from that of any other locality. The two collections, 4354 and 4356, have the following distinguishing characters: calyx tips terminal; ovary conspicuously red-papillate; hypanthium with red flush; flowers small.

10. *Goose Neck Creek*

The Goose Neck Creek locality is about one mile northeast of Dollar Bay. A large colony of *Oenothera* was found on the open bank of the creek after it had emerged from a wooded gorge. The single type, which was collected under number 2687, has the following characters: calyx tips terminal; ovary conspicuously red-papillate; hypanthium yellow; buds shorter than bracts; stem, ovary, bud cone, and hypanthium conspicuously pilose; bracts without wine-red markings on back.

11. *Pilgrim River*

The Pilgrim River location is about two miles southeast of Houghton. The railroad right of way here provided a disturbed habitat favorable for a large population of evening primroses. The collections revealed two distinct types to be present: (1) 3595: same as West Bluff 1043. (2) 3595a: same as Phoenix Mine 2052.

12. *Canal Road*

This locality is about one mile west of the village of Houghton near the present site of the Bosch Brewery. An *Oenothera* population occurred between the road and the railroad on a strip of land largely overgrown with weeds. A single collection, number 2241, proved to be a distinct type. Its distinguishing features are: calyx tips subterminal; inflorescence not declinate when young; bracts lacking a definite abscission zone; ovary conspicuously red-papillate.

BARAGA COUNTY

1. *Baraga*

This locality presented an artificial habitat on which *Oenothera* maintains a large population very successfully. It is an open stretch

of land along railroad tracks north of the town of Baraga. Here the surface disturbance so conducive to a large *Oenothera* population was caused by grading when the railroad was constructed. A sampling of the population revealed three distinguishable types, all of which have been found elsewhere: (1) 4315: same as Phoenix Mine 2052. (2) 4337: same as West Bluff 1043. (3) 4338, 4341: same as Mandan 4431.

2. *Pequaming*

This locality is not in the Keweenaw Peninsula, but is included in order to provide a comparison with the population found on the opposite shore of Keweenaw Bay at just the same distance from the head of the bay. Pequaming is an abandoned lumbering town about eight miles north of L'Anse. It is dominated by a large sawmill no longer in operation. At the eastern edge of town there is a rather extensive open area largely covered with sawdust and overgrown with weedy plants. *Oenotherae* were conspicuous among them. A sampling of the large population gave four distinguishable types, as follows: (1) 4253: same as Dollar Bay 3883. (2) 4254: same as West Bluff 1043. (3) 4262, 4294, 4296, 4303: calyx tips subterminal, 2 to 3 mm. long; inflorescence not declinate when young; bracts without definite abscission layer; ovary not conspicuously red-papillate, not densely gray-pubescent. (4) 2041, 4253, 4261, 4262, 4287, 4290, 4293, 4304: same as Mandan 4431.

At the twenty-two localities described twenty-one different types were discovered which appear to have a genetic basis and to warrant systematic recognition in a critical flora. A more thorough collection in the area would certainly reveal additional types that are not accounted for here, and it is hoped that in the future more extensive work will be done in order to discover other entities.

I think it might be helpful to future workers in the area to have a summary of the foregoing data in the form of a key constructed for the twenty-one types that were distinguished. I am especially indebted to Professor H. H. Bartlett, of the University of Michigan, for valuable assistance in the preparation of this key:

A. Calyx tips terminal

B. Ovary conspicuously red-papillate

C. Hypanthium with red flush; flowers small (St. Louis Hill 4354, 4356)

- C. Hypanthium not reddish; flowers medium
- D. Buds shorter than bracts
 - E. Back of bracts, hypanthium, and bud cone with some red papillae (Otter Lake 3579)
 - E. Back of bracts, hypanthium, and bud cone without red papillae
 - F. Stem, ovary, bud cone, and hypanthium conspicuously pilose
 - G. Bracts densely pilose on white nerves below, with subglabrous, wine-red areas between veins (Otter Lake 3861b)
 - G. Bracts without subglabrous, wine-red marking on back (Goose Neck Creek 2687)
 - F. Stem, ovary, bud cone, and hypanthium only moderately pilose (Dollar Bay 3883; Pequaming 4253)
- D. Bracts shorter than the buds
 - H. Some red mottling and red-based papillate hairs on bud cone (Otter Lake 3861a)
 - H. Bud cone not red-mottled nor red-papillate (Mandan 4431; Fort Wilkins 2522; Lake Upson 3797; Houghton 4235; Lake Linden 3662, 3663, 3664, 3665, 3665a, 3666, 3667, 3669; Dollar Bay 3866, 3868, 3878; Otter Lake 3818, 3832, 3861a; Big Traverse Bay 3661; Bear Lake 1231; Silver Mountain 2298, 2620; Baraga 4338, 4341; Pequaming 2401, 4253, 4261, 4262, 4287, 4290, 4293, 4304)
- B. Ovary not conspicuously red-papillate
 - I. Ovary densely gray-pubescent (Dollar Bay 3876; Houghton 4233)
 - I. Ovary not densely gray-pubescent
 - J. Bud cone with 8 stripes of purple splotches (Dollar Bay 3874)
 - J. Bud cone without 8 stripes of purple splotches
 - K. Calyx tips of mature buds 5 to 7 mm. long; stem conspicuously red-papillate (Houghton 4440)
 - K. Calyx tips of mature buds 2 to 4 mm. long; stem not red-papillate (Dollar Bay 3870; Bear Lake 3999)
- A. Calyx tips subterminal
 - L. Inflorescence declinate when young
 - M. Ovary conspicuously red-papillate, especially toward apex
 - N. Hypanthium red (Great Sand Bay 2770, 3806)
 - N. Hypanthium not red
 - O. Ridge at back of bract with red papillae extending onto it from stem ridge (Jacobsville 3602)
 - O. Ridge at back of bract without red papillae (Bete Gris Bay 3684; Jacobsville 3597; Big Traverse Bay 3660)
 - M. Ovary not conspicuously red-papillate
 - P. Hypanthium red (Eagle River 4832)
 - P. Hypanthium not red
 - Q. Ovary very densely and hypanthium densely viscid-pubescent, both pilose but with no visible crispate short pubescence among the pili (West Bluff 1043, 2443, 3789; Baraga 4337; Pilgrim River 3595; Pequaming 4254)
 - Q. Ovary almost lacking viscid pubescence, but with dense crispate

pubescence among the pili. Hypanthium only moderately viscid pubescent (Phoenix Mine 2052; Baraga 4315; Pilgrim River 3595a)

- L. Inflorescence not declinate when young
- R. Bracts with definite abscission zone (Houghton 4438a)
- R. Bracts without definite abscission zone
- S. Ovary conspicuously red-papillate (Canal Road 2241)
- S. Ovary not conspicuously red-papillate
- T. Calyx tips 0.5 to 1.0 mm. long; ovary densely gray-pubescent (Eagle River 4375)
- T. Calyx tips 2 to 3 mm. long; ovary not densely gray-pubescent (Pequaming 4262, 4294, 4296, 4303)

Other arrangements of the distinct entities would have been equally logical. It must be remembered that in *Oenothera* very widely different and true-breeding types may have exactly the same parentage. New types may come into existence by mutation as well as by hybridization, and such types may carry their distinctive genes in one of two complementary gametes, which sometimes function only as eggs, or only as sperms. Entities which appear to be very similar may actually have less in common, genetically, than others which seem widely unlike.

Under these circumstances it is more or less by arbitrary choice that one makes key distinctions. Others might be equally logical. From the standpoint of practical systematics it is best to avoid dependence upon features of growth habit and branching, which herbarium specimens of such large coarse plants can seldom show, but, rather, to rely upon the more minute distinctions which may be apparent in any herbarium specimen collected at flowering time. So far as there is evidence, many true-breeding and distinctive *Oenotherae* are extremely local. How many of them it may be practicable to distinguish does not yet appear, and only further studies such as the present one will indicate it. An effort to apply similar criteria at other localities may suggest what types or groups of types are most wide-ranging, and, therefore, from the standpoint of practical floristics, are most worthy of naming.

BERMUDIAN MARINE VAUCHERIAS OF THE SECTION PILOBOLOIDEAE*

WM. RANDOLPH TAYLOR AND ALBERT J. BERNATOWICZ

WHEN, during the spring of 1949, the writers undertook their studies of the marine algal vegetation of Bermuda, it was recognized that quite unexpected little problems might arise to deflect attention from the primary objects in view, and might well prove of considerable worth. This has certainly been true of a search started near the aquarium at the village of Flatts, directed toward finding good material of the marine *Dichotomosiphon*, which Collins and Hervey (1917) had reported from the inlet to Harrington Sound immediately adjacent to the aquarium grounds. The vaucheriacous plant which was particularly observed formed abundant aplanosporangia, but unlike those of *Dichotomosiphon*, and obviously of a diffuse species unknown at Bermuda. A similar plant has been reported from Connecticut, but was known to the authors only by repute (Taylor, 1937, p. 101). Sexual reproduction was only belatedly and sparsely found in preserved material. Consequently, in the winter period of 1950-51 the junior author made special efforts to locate this delicate *Vaucheria* at the original and many other localities, and was successful at several of them. Cultures were established, and it then became apparent that not one but two species were involved, both in the same section of the genus. One, *Vaucheria piloboloides* Thuret (1854), we shall describe and illustrate from our preserved material, since no such detailed observations have ever been reported from American material. The other species, which we propose to name *Vaucheria bermudensis*, was thoroughly studied both from preserved material and from plants brought to Michigan alive and fertile. It differs in many details, as will shortly appear.

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In Bermuda these two *Pilobolus*-like species of *Vaucheria* are common inhabitants of sandy bottoms in quiet waters. In areas containing much black decaying organic matter, as at Coopers Island, the sand is soft and suggestive of gritty mud. Here they form fine, diffuse patches one to two centimeters high and several square meters in extent; they climb over the occasional stones, which they tend to bury by the accumulation of sand among the filaments. In cleaner situations, as at a small unnamed cove on the north side of Smiths Island, the bottom is firmer, and the colonies (in this case *V. piloboloides*) bind the sand to form hemispherical domes 1.5–2.0 dm. in diameter, but the filaments clear of the sand are not longer than those on softer substrata. The upper portions of the colonies in either habitat are laid bare at low tide, whereupon they lie flat as a green film, but the capillarity of the sand never permits the exposed portions to become dry. At low tide no part of the colony is more than two decimeters below water, and at the lowest tides all or practically all the growth is exposed. These plants are common and widespread at Bermuda throughout at least the first half of the year. While they can be distinguished with tolerable ease from other *Vaucheriae* known to occur in the area, they cannot be distinguished from one another except in the presence of the sexual fruiting structures.

Fruiting material was difficult to recognize in the field because obscured by grains of sand, which were unavoidably lifted with the specimens to be examined. Furthermore, freshly collected material was rather scantily in fruit at this season. However, when kept in white enameled trays on outdoor aquarium tables and continuously but gently bathed by running sea water for from several days to three weeks, the plants fruited abundantly, the numerous fertile tips being silhouetted against the white trays and appearing as dark-green areas capping the vegetative growth.

The Bermudian plants of *Vaucheria piloboloides*¹ resemble the

¹ Stations for *V. piloboloides* Thur., which were confirmed by material with mature oöspores include: Wells Bay, Coopers I., no. 50-427, 8 Dec. 1950; cove on the north side of Smiths I., no. 51-839, 2 Feb. 1951; near the Bermuda Biological Station, St. Georges I., no. 51-626, 8 Jan. 1951.

European type rather closely. The irregularly branching filaments, 26–66 μ in diameter, bear the reproductive organs near the tips. In general, one antheridium and an oogonium appear close together, the latter overtopping the former. The antheridium seems always to be initiated first, but it does not necessarily discharge its antherozoids before the oöspore has appeared and matured (compare Pl. I, Figs. 1, 2 with 5, 6). Between the antheridium and the green vegetative filament there is cut off a cell which does not become inflated, but which retains the diameter of the filament or even collapses a little. It soon becomes empty and colorless. In length it is usually nearly twice the diameter, occasionally to more than three times. The antheridium is at first cylindric-lanceolate to spindle-shaped (Pl. I, Figs. 6, 7), but with maturity generally becomes stouter, a little inflated, and irregular because of the development of the lateral discharge pores, which are generally prominent or even tubular, and single (Pl. I, Figs. 4, 8, 9), sometimes two (Pl. I, Fig. 2), sometimes obscure (Pl. I, Fig. 1). Rather frequently, but not uniformly, a pore opens at the apex as well. The length ranges from 160 μ to 200 μ ; the diameter, exclusive of the pore tubes, from 30 μ to 45 μ .

The oogonial branchlets always arise close below the antheridial supporting cells. They grow as erect clavate structures, which enlarge rapidly and become sharply inflated at the summit (Pl. I, Figs. 1–4). A cross wall is then formed a short distance up the stalk portion, and the withdrawal of the cytoplasm toward the distal end follows. The fertilization pore is obscure but probably terminal. The fertilized egg develops a compact form at the distal end of the oogonium and, after fertilization, a firm but not very thick oöspore wall; it is securely anchored to the wall of the oogonium by a zone of attachment perceptibly below the end of the spore. The diameter of the lowermost stalk portion of the oogonium after spore maturation is that of the filament, but increases somewhat upwardly for about one half to two thirds of the total length, where the oogonium is sharply inflated to form the nearly spherical summit. There is rather frequently a sharp ring about the stalk near the inflation (Pl. I, Figs. 5–7), apparently a thickening of the wall, but no septum has been seen to accompany this ring. The length of the mature oogonium ranges from 320 μ to 500 μ , the diameter from 140 μ to 210 μ , averaging 380 $\mu \times$ 161 μ . The oöspores are peculiar, not only in giving the characteristic *Pilobolus*-like aspect to the oogonia, but in being somewhat compressed (Pl. I, Figs. 10–14). Spores for meas-

urement must be carefully selected because they tend to be pushed out of alignment by any pressure on the oogonia. From several measurements we secure a range in length of 75 μ to 110 μ ; in transverse diameter, of 105 μ to 145 μ . The mean length is 85.7 μ , and the standard deviation is 8.4 μ . The mean diameter is 119.3 μ , and the standard deviation is 12.4 μ . The ratio of spore length to spore diameter averages 1:1.39. Correspondingly, the ratio of spore diameter to oogonium diameter averages 1:1.35.

Unfortunately the available European citations of this species are very niggardly in data. The brief original description (Thuret, 1854, p. 389) carried no illustration; the localities given are on the Channel coast of France. Kützing (1856, p. 20, pl. 55, fig. 1) described a similar plant from near Brest as *V. fuscescens*. Walz (1866) in his monographic paper does not figure the species, but puts *V. fuscescens* in synonymy. Though our plants showed less elaborately branching clusters of fruit than did those figured by Woronin (1869, pl. 2) from the Mediterranean coast of France, they agree well in other respects. Le Jolis (1864) quotes Thuret at some length to amplify and add to the original description, but figures only the aplanosporangium and, imperfectly, the oogonium, being on the whole less informative than Woronin. Ernst (1904) gives excellent figures of aplanosporangium formation and germination at Naples, but does not discuss the sexual reproduction, whereas Migula (1907, p. 874) ascribes the plant to the Adriatic, these two stations suggesting warm-water affinities. Heering (1921), however, records it from Warnemünde² on the western Baltic coast of Germany. Doubtless there are other European records, but the species apparently is not abundant enough to have been very critically studied and measured, since Hamel (1931, p. 428, figs. 33, II, 33, III) copies Woronin's old figures, and Dangeard (1939) furnishes neither new figures nor data.

So far as the American record² is concerned, it is based on Collins' specimen no. 476 in the Phycotheca (1898), which the senior author attempted to study microscopically, but failed to revive sufficiently. Collins' variety *compacta*, published as no. 477 in the same collection,

² After this paper had been submitted for publication Cand. mag. Tyge Christensen (København), who has studied the genus extensively, kindly informed us that the Warnemünde record was based on Hauck et Richter: *Phyk. Univ. no. 282*, but that the material had been misidentified. It consists of a dioecious species, apparently the one which Collins similarly confused with *V. piloboloides* in *Phyc. Bor. Am.*, the correct name for both being *V. compacta* (Coll.) Coll.

he later came to consider a distinct species, but the original collection likewise proved obdurate. Brown (1929), monographing the American members of the family, seems to have had nothing to add from personal observations on these particular species. She includes "Asiatic Sea" in the list of localities, but this is probably an erroneous substitution for Adriatic Sea, rather than a range extension.

In our investigation it soon became evident that there are two entities in the Bermudian material, the second of which, unless oöspores are present, cannot be distinguished from *V. piloboloides*. When the spores are present, their size relative to the oögonia and their proportions make them readily distinguishable. With one possible exception, there is no other species with characters which come at all close, since the habit of growth, spherical spores, and scattering of the sex organs seem to rule out *V. compacta*. The possible exception is *V. longicaulis* Hoppaugh (1930) from mud flats in Monterey County, California. Dr. Hoppaugh, however, definitely states that in *V. longicaulis* the oöspores are subspherical, which they clearly are not in *V. bermudensis*, and she figures them as free from the oögonial wall, which they are not at any stage short of final release in either *V. piloboloides* or *V. bermudensis*. In respect to the antheridia, she states that the usual number of projecting pores is five to eight, whereas in our plant it is usually one or two, and very rarely more.³ It would have been much more satisfactory if Dr. Hoppaugh had given a good series of measurements of mature spores, but she expresses distrust of such data, basing her position on uncertainty regarding maturity. We found no difficulty in regard to spore maturity, for the light-brown spore wall was thick enough to be distinctive in both species. The spore sizes also held close to the average for the species. The variation in oögonial size appeared to us to be considerable, contrary to her findings in *V. longicaulis*, although the general shape was in most cases distinctive.

The colonies of *V. bermudensis* are diffuse and appear as very light green clouds of filaments, through which the sand below readily appears. The lower, older, filaments ramify among the grains of sand. They are frequently septate (Pl. II, Fig. 2), but the younger filaments are not (Pl. II, Fig. 1). Rather frequently sharp inflations

³ In one specimen, without oögonia, occurring in a unique stagnant salt-water pond on Paget Island, antheridia bore several discharge pores, but it was not possible to establish any connection with identifiable material of this or any other species.

of the main filament axes or of side branches occur without distinctive contents, but these are considered abnormalities (Pl. II, Fig. 5). Among the filaments near the substratum one sometimes finds those in which a very deep green color is particularly evident and which are inflated at the ends, sometimes simply (Pl. II, Fig. 3), sometimes digitately (Pl. II, Fig. 4), sometimes with much longer branches. These have very dense cytoplasm and reduced vacuoles, yet may show cyclosis. It may be suggested that they are some sort of perennating organ, but, since no wall segregates them, one can hardly consider them equivalent to akinetes. Certainly they are not malformations due to injury.

As fruiting time approaches, the tips of the rather simple young erect branches become clavate, and the terminal spores are cut off by transverse walls (Pl. II, Figs. 6-9). A few empty sporangia were seen, and a few germinating spores, which almost certainly were aplanospores, but the process was not studied in detail. The aplanosporangia were observed to germinate and form a filament from the tip without first being discharged, but this was rare. The axis could grow forward from below an aplanosporangium to form a new actively growing tip.

The antheridia appear in a culture somewhat later than the aplanosporangia and independent of them. Both the terminal fertile cell and the supporting cell below it are at first green, but the latter soon appears empty. Its lateral walls seem thin and tend to collapse readily, so that the end walls often curve into it because of the turgor of the adjoining green parts. This cell is seldom shorter than its breadth, but equally seldom it is more than twice as long (Pl. II, Fig. 11), the dimensions being $18\ \mu$ to $50\ \mu$ in diameter and $25\ \mu$ to $65\ \mu$ in length, with the average about $34\ \mu \times 42\ \mu$. Typical cases appear in Plate II, Figures 12-17. The rare exceptions were especially studied, and consequently the figured examples are rather numerous. A plant in which the antheridium is subtended by a single wall, yet apparently functioned normally, shows in Plate II, Figure 12, and another with a very oblique wall in Plate III, Figure 3. These were less common than cases in which three walls and hence two supporting cells appear (Pl. III, Figs. 2, 5, 6), of which the lower commonly retains a little chlorophyll.

Early in the period of sexual activity, and particularly in some examples, only antheridia occur. Under such circumstances they

are especially liable to follow one another in succession, an erect outgrowth from below the first antheridium developing a second antheridium a bit higher, succeeded by another in turn (Pl. II, Figs. 10, 12). It was otherwise rare to find a second antheridium developed before an oogonium appeared. Such male plants could not be identified with certainty, but it cannot be assumed that they represent a dioecious species. More probably they are simply cases of delayed development.

Since the senior author saw only incompletely developed plants in the field and since his junior colleague was too preoccupied with other tasks to give sufficient time to it, details of cell division in the development of antheridia and antherozoids were not followed. The antheridia are at first nearly cylindrical (Pl. II, Figs. 10-12), later more nearly spindle-shaped, very often with the distal end somewhat extended and curved to one side (Pl. II, Figs. 13, 14). The subtruncate tip commonly, but by no means always, acts as a discharge tube (compare Pl. III, Figs. 2, 4, 5 with Figs. 3, 6, 7). There is practically always at least one lateral discharge pore (Pl. II, Figs. 14, 15; Pl. III, Figs. 2, 3, 5, 7) and perhaps more usually two (Pl. II, Figs. 16, 17; Pl. III, Figs. 4, 6). The formation of abortive pores (Pl. II, Fig. 13) was not often noted. In only one collection, entirely without oogonia and so not to be identified, did we find very elongate multipored antheridia. Discharge pores are nearly always elevated, sometimes into short (Pl. III, Fig. 2), sometimes into longer (Pl. II, Fig. 15; Pl. III, Figs. 4, 7) tubular projections, but the average lies somewhat between.

The dimensions of the antheridia vary a good deal, and more so in the absence of oogonia. The figures from identifiable samples show a range in diameter (excluding discharge tubes) of $26\ \mu$ to $50\ \mu$; in length, from $219\ \mu$ to $464\ \mu$, with averages about $38\ \mu \times 331\ \mu$.

Oogonia were formed abundantly in two samples. The senior author was able to study preserved material of these, and of living specimens brought back in February, 1951, and to confirm and extend the observations made in the field by the junior author. Oogonia were not observed except in succession after the appearance of antheridia. The formation of two pairs of organs on a filament was not common. The antheridium sometimes matures before the oogonial branch is well developed, even to the point of discharge; sometimes it delays and the oöspore matures while the antheridium

still has no discharge pores. The outgrowth of the filament comes from below the antheridial supporting cell (Pl. III, Fig. 1), sometimes close, sometimes far down the filament, turns sharply upward, far exceeding the antheridium, and is cut off by a wall at about the mid-height of this structure (Pl. III, Figs. 4, 5). Rarely one of the ordinary filament cross walls appears in the oögonial branch (Pl. III, Fig. 7) or below the antheridium (Pl. III, Fig. 2). The cytoplasm in the oögonium then contracts, maintaining its contact very tenaciously with the distal end wall of the oögonium, leaving behind an essentially protoplasm-free space. Rather often a line, usually a little irregular, is visible on the oögonial wall about halfway up (Pl. III, Figs. 5, 7, 11). In a few plants the protoplasm could be clearly seen to pass this line and demonstrate the absence of a septum. In others there was reasonable assurance that a septum was present, and yet the lower cell thus formed contained little protoplasm, and so was probably segregated after the bulk of the cytoplasm had retracted toward the tip. This condition may represent the last trace of a tendency to form an oögonial supporting cell.

Most of the oögonia seen were either rather young or with mature oöspores. In the living as well as in the preserved material some examples did show what may be interpreted as the receptive stage for fertilization. The oögonial protoplasm then lies strictly at the end of the oögonium. No clear wall could be detected across the tip, but a little to the side the wall appears, closely encircling the cytoplasm, which even seems to project just a little. The oögonial protoplasm shows little suggestion of a central vacuole at the time, and has a fairly well defined lower border, with the chromatophores generally disposed except at the small area closely encircled by the wall, which is the clear gray of alveolate cytoplasm and may be the receptive region.

When the oöspores are mature, the oögonial wall continues to adhere. Consequently, whatever exists beyond the equator of the spore seems a part of the spore wall. Among great numbers studied no spore was seen loose in its oögonium (though pressure deformations of the oögonium may give such a first impression falsely), and no instance of spore discharge was observed.

The shape of the oögonium must be contrasted with that of *V. piloboloides*. The stalk portion of the oögonium of *V. bermudensis* enlarges somewhat more considerably, but at about three fifths of

the distance from the base it ceases to swell and extends up to the equator of the spore without much further increase. Sometimes this is markedly a sharp change in contour (Pl. III, Figs. 4, 6, 7), generally it is less sharp (Pl. III, Figs. 9, 10), but a little loss of turgidity or displacement in mounting will conceal this feature, which is otherwise evident to the critical eye. The oögonium so produced is distinctive in shape and is much less inflated than that in *V. piloboloides*. Though the typical shape of the oögonium in *V. piloboloides* is in the fullest expression nearly spherical on a cylindrical stalk, in *V. bermudensis* it may be better described as turbinate. The oögonial wall of the inner tapered portion is thin and smooth; that of the outer portion near the spore can be seen under intense illumination through a very small diaphragm aperture to be a little thicker (or more refractive) and to be obscurely, irregularly, and rather coarsely rugose. The dimensions of the oögonia range in diameter of the outer end from 116 μ to 153 μ , and in length from 285 μ to 510 μ , the average being about 131 μ by 388 μ .

The oöspores are depressed-spherical to transversely elliptical (Pl. III, Figs. 6-13), with a brown apparently simple smooth wall about 2 μ thick, although a very few with a clear refractive wall 4 μ thick were seen. Usually the portion beyond the equator or zone of greatest diameter is about hemispherical. Unless the spore is viewed strictly from the side, this is not evident. The diameter of the oöspores ranges from 105 μ to 141 μ , with the mean about 120 μ and the standard deviation 8.4 μ . The oöspore length has a range from 90 μ to 136 μ , and its mean is at 105 μ , with the standard deviation 8.5 μ . The ratio of spore diameter to oögonium diameter averages 1:1.08 (compare with the ratio of 1:1.35 in *V. piloboloides*). The ratio of spore length to spore diameter averages 1:1.15. To compare this ratio with the oöspore proportions of *V. piloboloides*, 1:1.39, we have calculated the statistic *t* and found it to be 11.6 (degrees of freedom = 61) (Snedecor, 1946). The probability of getting such a large value of *t* is less than one in one thousand, if we assume that only one population furnished both groups of collections (Fisher and Yates, 1949). The indication is strong, therefore, that the two groups of samples which furnished the oöspore ratios represent two distinct populations.

We therefore offer a technical description of this new plant as: *Vaucheria bermudensis* sp. nov.—Tabb. II-III.—Plantae colonias dif-

fusas formantes; filamenta 18–51 μ diam., irregulariter patenterque ramosa; rami sporangiales clavati; aplanosporangia clavata ad obovata, 80–110 μ diam., 212–240 μ long. Antheridia primum in ramo terminalia, in cellula vacua sustinente portata, subcylindrica ad subfusiformia, 26–50 μ diam., 219–464 μ long., 1–2 poris lateralibus praedita. Oögonia turbinata ad clavata, stipitata, e situ infra antheridia singulatim orientia necnon haec superantia, a filamentis per septum sejuncta, 285–510 μ long., 116–153 μ diam., prope fastigium paululum expansa. Oöspora in latere inferiore subcompressae, 105–141 μ diam., 90–136 μ long. Specimen typicum in loco dicto Shore Hills, St. Georges I., Bermuda, legit A. J. Bernatowicz no. 51–790, 27 Jan. 1951.

Vaucheria bermudensis sp. nov.—Plates II–III.—Plants forming diffuse colonies; filaments 18–51 μ diam., irregularly and patently branching; sporangial branches clavate; aplanosporangia clavate to obovoid, 80–110 μ diam., 212–240 μ long. Antheridia at first terminal on a branch, borne on an empty supporting cell, subcylindrical to subfusiform, 26–50 μ diam., 219–464 μ long, with 1–2 lateral pores. Oögonia turbinate to clavate, stalked, arising singly from below the antheridia and overtopping them, separated by a cross wall from the filament, 285–510 μ long, 116–153 μ diam., slightly expanded near the tip. Oöspores generally somewhat compressed on the lower side, 105–141 μ diam., 90–136 μ long. Type specimen from the well of the tide gauge at the Bermuda Biological Station, Shore Hills, St. Georges I., Bermuda, collected by A. J. Bernatowicz no. 51–790, 27 Jan. 1951.

Additional stations for *V. bermudensis* which were confirmed by material with mature oöspores include: Flatts, near the government aquarium, on Hamilton I., no. 49–173, 9 March 1949 and no. 49–880, 22 April 1949; Vaughans Bay (also called Whites Bay) on the east end of St. Davids I., no. 51–718, 20 Jan. 1951.

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EXPLANATION OF PLATE I

Vaucheria piloboloides

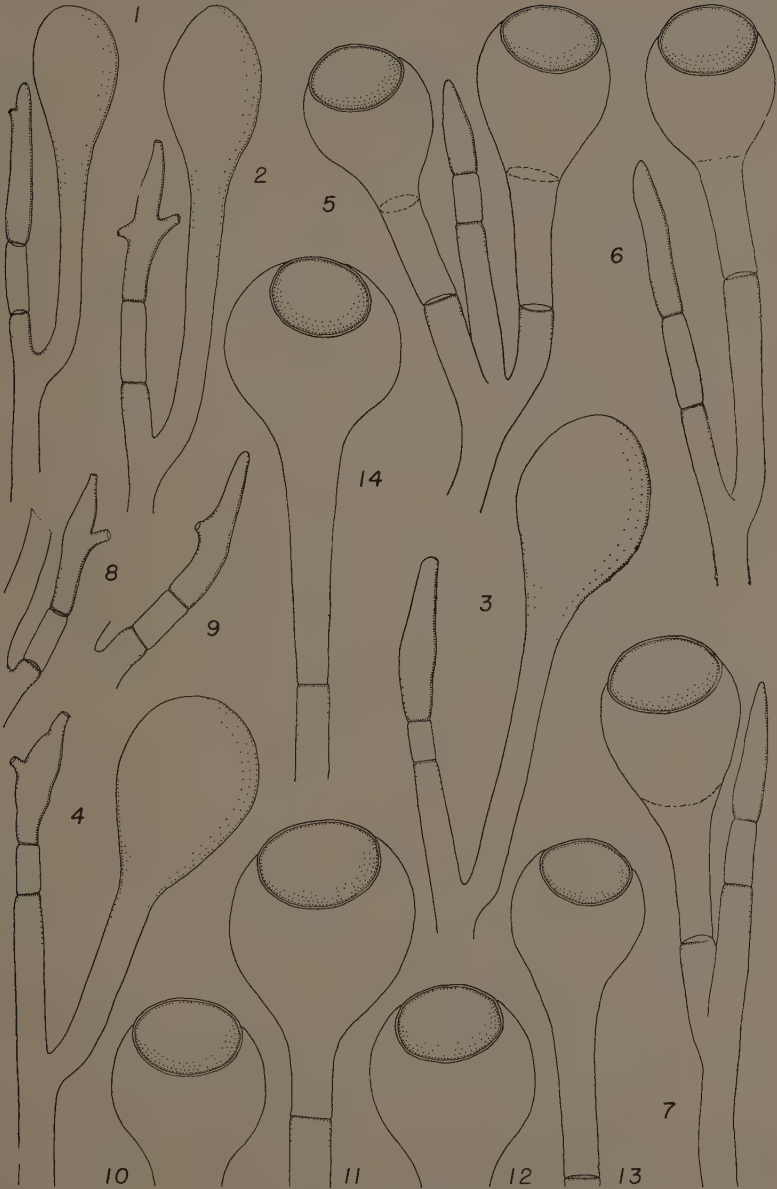
(All figures $\times 140$)

FIGS. 1-4. Branchlet tips with young oögonia. The antheridium in Figure 3 has not yet developed discharge pores, but those in the other figures have matured

FIGS. 5-7. Branchlet tips with mature oöspores in the oögonia; here also the antheridia are young

FIGS. 8-9. Individual mature antheridia

FIGS. 10-14. Individual mature oögonia with oöspores



Vaucheria piloboloides

EXPLANATION OF PLATE II

Vaucheria bermudensis

(All figures $\times 100$ except as marked)

FIG. 1. A young portion of a branch system (a short section omitted to save space) showing alternate branching

FIG. 2. An old portion of such a system, showing cross walls

FIGS. 3-4. Tips of lower branches with congested contents. $\times 140$

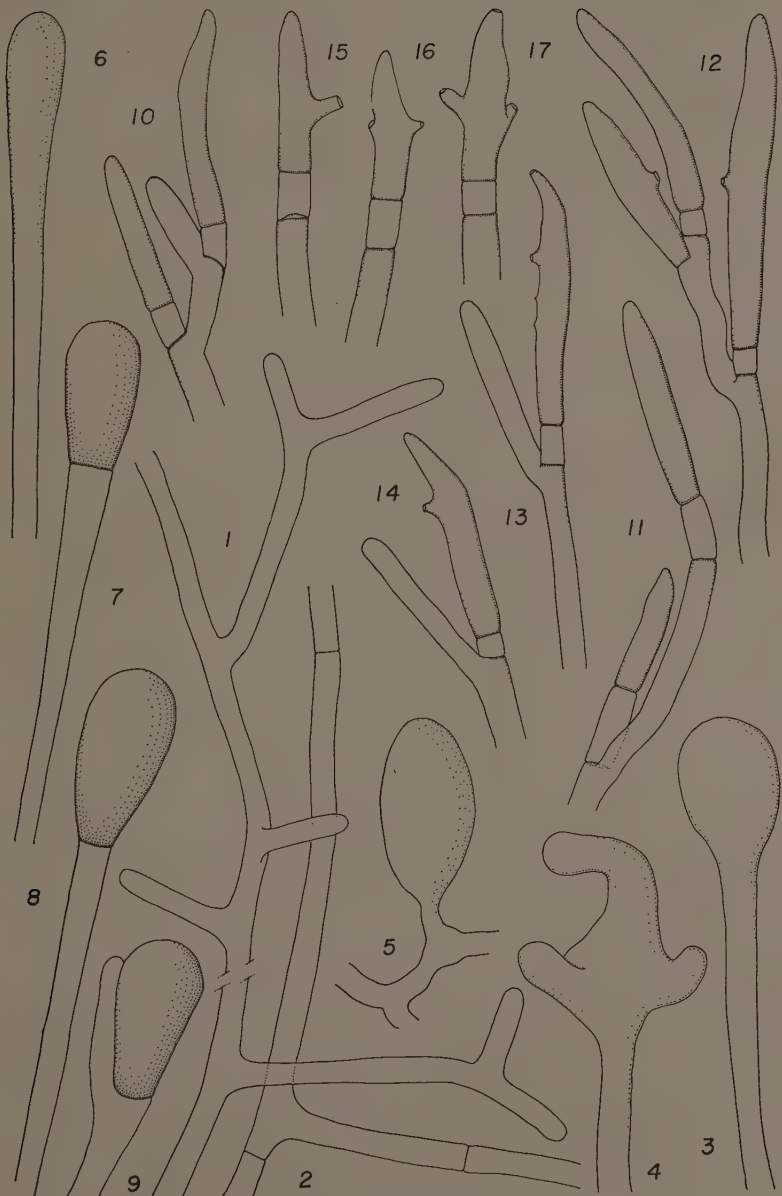
FIG. 5. A short vesicular lateral branchlet, considered an abnormality

FIGS. 6-9. Stages in the development of aplanosporangia from erect branch tips

FIGS. 10-11. Young branch tips showing development of successive young antheridia

FIGS. 12-14. Similar tips with mature antheridia

FIGS. 15-17. Mature antheridia as associated with oögonia. $\times 140$



Vaucheria bermudensis

EXPLANATION OF PLATE III

Vaucheria bermudensis

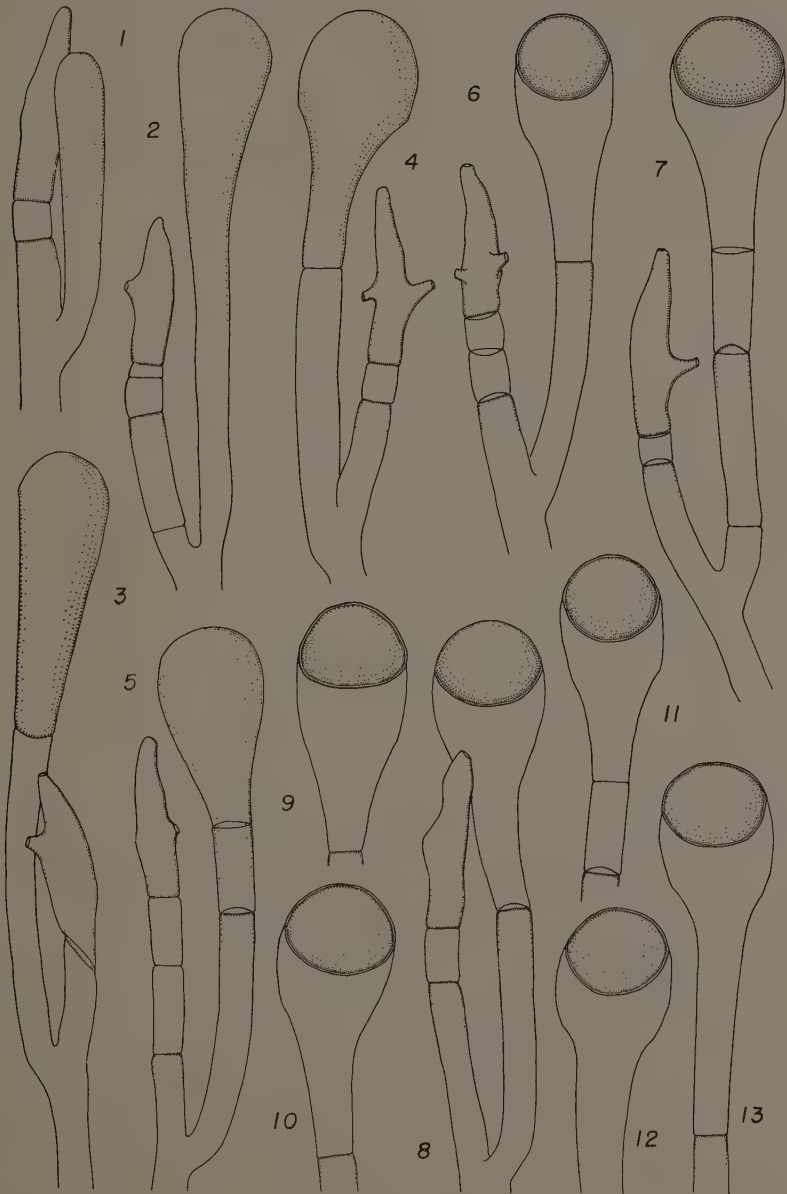
(All figures $\times 140$)

FIGS. 1-2. Young stages in the development of an oogonial branchlet

FIGS. 3-5. Somewhat later stages, with the segregation of the oogonium completed

FIGS. 6-8. Branchlets with mature antheridia and mature oöspores

FIGS. 9-13. Mature oöspores in their oogonia



Vaucheria bermudensis

CYSTOPTERIS BULBIFERA (L.) BERNH., A CONVENIENT SOURCE OF APICAL CELLS FOR SLIDES

KATHARINE TRYON

BOTANISTS who teach classes in morphology and who are interested in the apical cell of the Pteridophytes usually find it difficult to demonstrate this phenomenon in stems. Two things primarily contribute to the problem. First, the growing apex of a rhizome is almost impossible to find in many temperate-zone ferns, and, second, the apical cell is likely to lie in a considerable mass of tissue. These difficulties are usually circumvented by using the root, which is smaller and in which the apical cell can be quite easily found in sections. Even when roots are used, the fern must still be dug up. The method suggested in this paper involves remarkably little effort beyond locating a stand of the fern.

Cystopteris bulbifera (L.) Bernh. is a cosmopolitan species. Specimens collected from many areas in the eastern and central United States are included in the University of Michigan Herbarium, and among them are examples from seventeen different locations in Michigan alone, representing a range covering nearly the entire state. The plant appears to grow in more or less isolated communities or clumps. It has been collected by the writer in Reese's Bog on the west shore of Burt Lake in Cheboygan County, Michigan, where it tends to grow in open areas on the otherwise densely shaded bog floor. It has been most frequently collected by others along stream banks in the shade, and on shady limestone cliffs. Generally speaking, the fern grows well in a variety of habitats.

C. bulbifera is easily recognized by the elongated older fronds with many fleshy-scaled buds, or bulbils, attached to the lower surfaces (Pl. I, Figs. 1-2). The bulbils average from four to five millimeters in diameter when fully developed.¹ Size seems to bear no relation to maturity, for small ones grow into new plants as readily

¹ Matouschek (1894) and Rostowzev (1894) have both described these bulbils in detail.

as do large ones. Fully developed bulbils of all sizes are present on the fronds as early in the season as late June. They fall off very easily, and many germinate at once, producing new sporophytes in the same season that they themselves are formed. These adventitious buds apparently constitute the only means of reproduction of the fern, since the writer's own and all other reported attempts to germinate the spores in the laboratory have failed.

When dissected and examined, the bulbil of *C. bulbifera* is found to consist of from two to five fleshy scales attached at the base to a very small tomentose "axis." If the buds are placed in damp chambers on moist paper, or in wet sphagnum, roots develop perceptibly from the basal end within four or five days. These roots are followed by the appearance of a young leaf at the apex. Usually just one leaf is first formed by a single bulbil, and it will reach a length of several centimeters before another appears. Because of the abundance of stored starch in the fleshy scales, these young plants will grow for at least six months on moist paper alone. In petri dishes they are easily maintained, since they are not readily subject to attack by fungi. In sphagnum in the greenhouse new sporophytes can be grown to considerable size, and a crop of bulbils can be harvested from them in five months or less. The writer has kept two six-inch pots of the fern for nearly two years, collecting bulbils at intervals. Buds can also be stored at 10° C. for at least eighteen months with only a slight loss of viability.

After the germinating bulbil has grown for six weeks, the young "axis" or growing rhizome in the center has enlarged sufficiently to be handled. It can be dissected away from the attached scales and killed and fixed for sectioning. Longitudinal sections of this young rhizome show its own apical cell as well as those belonging to the adjacent leaf primordia and the apical cells of roots emerging at the basal end. A particular advantage of this material is that one set of sections will usually provide both transverse and longitudinal cuts of apical cells. These are not, for obvious reasons, always in perfectly vertical or horizontal planes, but most of the sections will be quite usable (Pl. I, Figs. 3-4). Root apical cells with four cutting faces, and stem apical cells with three, can sometimes be found on the same slide.

The procedure used to prepare slides of this material is not difficult to follow. Randolph's modification of Nawaschin's solution as

given by Johansen (1940) yields good fixation in twenty-four hours. Dehydration in tertiary butyl alcohol as recommended by the same author left the material soft enough to cut easily, and embedding in paraffin presented no difficulties. Sections were cut at fifteen microns; twelve would probably be slightly better. Bleaching with hydrogen peroxide before staining tended to improve the preparations. Sections were stained overnight in safranin dissolved in 50 per cent ethyl alcohol, with careful destaining in acidified 70 per cent alcohol. After the completion of the dehydration, they were counterstained for one-half to one minute with fast green dissolved in clove oil. Other combinations of stains, like iron hematoxylin and orange G, would probably give at least equally good results.

This method of preparing apical cell slides is so comparatively simple that it is surprising botanists have not used it more often. Large numbers of ferns produce sporophytic buds of one kind or another which could probably be used (Heinricher, 1878; Kupper, 1906), but most of these species are tropical forms usually available only as herbarium material. Also, in many instances, the buds are either not conspicuous, or are formed on the frond only when it is isolated from the parent plant. According to Sadebeck (1895), *C. bulbifera* is the only fern producing a prominent bud with large fleshy scales containing an abundant reserve food supply. *Phegopteris sparsiflora* Hook. which Sadebeck describes, also has conspicuous pairs of buds at the bases of the pinnae, but this plant appears to be limited to the East African flora. Besides *C. bulbifera*, the only North American species known to this author which produces an evident and accessible bud is *Camptosorus rhizophyllus* (L.) Link., the walking fern, whose fronds root at the tip. According to Kupper, the apical cell of this bud is difficult to demonstrate, although it can be done. Heinricher (1881) and Zimmermann (1881) both describe in detail the development of the bulbil of *Asplenium bulbiferum* Forst., which resembles that of *C. bulbifera* slightly, but is much smaller, and germinates while still attached to the frond. Straus (personal communication, 1951) has shown the writer excellent apical cell preparations from the bulbil of *Dryopteris prolifera* (Retz.) C. Chr., which, like *A. bulbiferum*, is a tropical species. These last two ferns, however, are often found in the United States in botanical-garden collections.

To judge from the extensive literature, all known sporophytic

buds on ferns develop by means of apical cells. These buds represent a greatly neglected source of material for classroom or other demonstrations of the apical cell type of growth, and *Cystopteris bulbifera*, as the most abundant northern hemisphere species with conspicuous adventitious buds, is suggested for preparing slides for this use.

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Cystopteris bulbifera (L.) Bernh.

FIG. 1. Side view of a bulbil attached to a frond (scale in millimeters)

FIG. 2. Three bulbils on fronds, very slightly enlarged

FIGS. 3-4. Transverse and longitudinal sections of apical cells. $\times 417$

FORESTRY

SOME RESUPINATE POLYPORES FROM THE REGION OF THE GREAT LAKES. XXIII*

DOW V. BAXTER

SURVEYS made from areas bordering the Bering Sea in Alaska to the Baltic Sea in Russia and from the Arctic Ocean to the Caribbean and from Swedish Lapland through most of Europe have resulted in a somewhat better understanding of the relationships and occurrences of the resupinate polypores on both continents. Overholts (11) has stated that at least 43 per cent of the species of the American pileate polyporaceae appear in Europe or in other parts of the Eastern Hemisphere.

Although lists of fungi from Europe and America might correspond in a broad pattern, differences between the floras become more apparent as one acquires an acquaintance with field environments on both continents. It is known, for example, that the almost ubiquitous *Ganoderma applanatum* (Pers.) Pat. grows in both places, but differences in its growth habits in Europe and in North America soon become obvious to the collector. In an afternoon's foray about Ann Arbor, for example, one can scarcely avoid seeing this fungus, and it appears with equal frequency over large sections, especially in the Middle West in this country. With the exception of a comparatively few areas, notably Denmark, I have rarely seen specimens of it in Europe outside herbaria. Another fungus, *Polyporus pargamentus* Fr., is common all over the State of Michigan, but I have never observed it in the territory extending from Lapland and Russia to south Bohemia. In Swedish hardwoods *Fomes robustus* Karst. is present on oak, but it does not occur on hardwoods about Ann Arbor. *Polyporus carneogilvidus* Romell likewise attacks oak wood in Sweden, though it has never been collected here. *Pol. vulgaris* Fr. *sensu* Romell, *Pol. sericeo-mollis* Romell and *F. annosus* (Fr.) Cooke may readily characterize a north European forest-fungus flora of an arboreal type closely related to many of our timberlands in the Upper

* Financial support for several plates presented in this paper has been given by the School of Natural Resources, University of Michigan.

Peninsula. Although *Pol. vulgaris* is represented in such a Michigan forest, it is not so prevalent as in the forests of Sweden about Stockholm.

In North America I have collected *Fomes annosus* in the Tongass National Forest of southeastern Alaska, where it is rather common, and in many regions of this continent, but nowhere in the northern forests of Alaska, Canada, or the United States does it appear as abundantly as in many conifer areas of Europe. Only in southeastern American localities (especially in the Piedmont country) does its occurrence suggest the abundance observed in plantations of Scotland, in many Swedish spruce forests, or those conifer timberlands of south Bohemia. These forests in Europe bear little resemblance to a juniper association of parts of the South Carolinian Piedmont. One is not reminded at all of South Carolina forest sites infested with *F. annosus* when observing stands where root rot appears over vast areas in Sweden or Norway. Certain soil factors and the fact that the land has been under cultivation prior to the present tree occupancy may, however, be analogous for some localities. Furthermore, it would be possible to make a sizable collection of polypores in a few hours from the Gulf States and in the Southeast that would be entirely unlike anything represented in Europe.

This paper discusses a number of North American and European polypores with special reference to their occurrence and distinguishing features. Because usual descriptions of the plants included here do not consider potential variations in appearances of the fruiting bodies when the plant is exposed to different field environments, the polypores are placed in groups 1 to 8 in Table I to facilitate their determination. *Poria flavomarginata* Murr., an allied southern plant, but characterized by minute pore mouths and spore sizes, does not belong to this culture group. It produces a greenish-yellow mycelium (Pl. IX).

Distinctions that pertain only to the significant gross morphological and the microscopic features of the plants are emphasized in the descriptions that follow the table. It is well known that isolates vary in texture and color of the rots even for the same species, but such entities retain their features for indefinite periods in cultures (2). There are, indeed, significant temperature-growth rate characteristics that are often marked. Where these are distinctive, forms (not species) are designated.

TABLE I
OCCURRENCE OF CERTAIN BROWN POLYPORES IN NORTH AMERICA

Fungus	Wood	Form distinguished by response in culture
<i>Fomes Arctostaphyli</i> Long	Arctostaphylos and other desert shrubs	
<i>Fomes igniarius</i> (L.) Gill	Populus (aspen), exceptionally on birch*	
<i>Fomes igniarius</i> var. <i>nigricans</i> Fries	Betula, Fagus, Acer, and other woods	
<i>Fomes pomaceus</i> (Pers.) Big. & Guil.	Prunus and others rosaceous hosts	
<i>Fomes pomaceus</i> var. <i>Crataegii</i> (Pers.) Baxter	Crataegus	
<i>Poria laevigata</i> (Fr.) Cooke	Betula and other hardwoods	 f. <i>prunicola</i> comb. nov. on Prunus.
<i>Poria spiculosa</i> Camp. & David.	Carya	
<i>Poria floridana</i> (Murr.) Sacc. & Trott.	Southern woods	Form I on <i>Quercus nigra</i> Form II on <i>Quercus phellos</i> Form III on <i>Carpinus</i> sp.
<i>Poria punctata</i> (Fr.) Cooke	On a great variety of hardwoods, but most common on Alnus, Rhus, Robinia, and Salix	
<i>Fomitiporia dryophila</i> Murr.	Southern woods	Form I mostly on <i>Quercus virginiana</i> Form II on <i>Nyssa biflora</i> Form III on <i>Liquidambar styraciflua</i>
<i>Fomes robustus</i> Karst.	Quercus and other hardwoods (also conifers in Europe)	f. <i>Tsugina</i> Overh. on <i>Tsuga canadensis</i> and <i>T. heterophylla</i> f. <i>Abietis</i> forma nov. on <i>Abies concolor</i> f. <i>juniperinus</i> forma nov. on <i>Juniperus</i> sp. f. <i>Taxodii</i> Baxter on <i>Taxodium distichum</i>

* See footnote 1, p. 96.

Fomes Arctostaphyli Long (on desert shrubs)

Typical fruiting bodies (Pl. I, Fig. 2) mostly less than 3 cm. broad, occurring on *Arctostaphylos* spp. Setae are not present. The rot does not exhibit distinct lines as does *Fomes igniarius* (13). *Fomes Arctostaphyli* differs culturally from *F. igniarius*, and is culturally and morphologically different from *F. robustus* (6). Differences between *F. Arctostaphyli* and *F. robustus* involve the larger size of the mature fruiting body and the lighter color of the pore mouths of the latter. A trace of red, usually present on the surface of the fruiting bodies of *F. Arctostaphyli*, is not to be seen in *F. robustus*.

Fomes igniarius (L.) Gill (on Populus Group I of Verrall [12])

Typical mature pileus (Pl. I, Fig. 1) larger than 3 cm. broad, mostly less than 15 cm. broad, rimose, on aspen, exceptionally on birch.¹ Pore diameter mostly $100.8\ \mu$ (Verrall), hyphae of context measure $4.45\ \mu$ (Verrall), setae are present. In ten days on malt agar *Fomes igniarius* grew more slowly (mostly less than 40 mm.) than did *F. igniarius nigricans* at the optimum temperature (27.5°C.). According to Verrall (12), this fungus produces a methyl salicylate odor in culture, but Nobles (10) says that the odor is slight in some and nonexistent in others.

Fomes igniarius nigricans Fries (on Betula group and species on other hosts, Groups II and III of Verrall [12])

Typical mature pileus (Pls. II, Figs. 1, right, 2, 3; V, Fig. 1; VII, Fig. 2, right) often large, i.e. larger than 3 cm. broad, often as much as 24.5 cm. broad (and therefore definitely larger than *Fomes Arctostaphyli* (Pl. I, Fig. 2) and ordinarily larger than *F. igniarius* (Pl. I, Fig. 1), growing in the eastern part of the continent but not necessarily averaging larger than *F. igniarius* on aspen in the Rocky Mountain areas), chiefly plane to convex, the surface usually cracking somewhat, but not ordinarily becoming rimose; chiefly on birch, beech, and maple.

Pore diameters are about the same for most collections on birch, i.e. $102.9\ \mu$, but are mostly larger on other hosts, $149.2\ \mu$ (12). Hy-

¹ Green standing aspen is by far the most common tree attacked. The only noteworthy exception encountered in the surveys made for this series of reports was in an area of aspen and birch growing on basaltum at the mouth of the Clearwater at the Athabasca River, Alberta, Canada. Here also the birch were seriously infected from the same fungus that was rotting most of the aspen in the stand.

phae of the context are smaller ($3.19\ \mu$) than those of *Fomes igniarius* ($4.45\ \mu$) (Verrall).

Cultures of *Fomes igniarius nigricans* (Pl. X) grow more rapidly than those of *F. igniarius*, but a methyl salicylate odor is not produced.

Fomes pomaceus (Pers.) Big. et Guill. (on Rosaceus hosts, especially Prunus)

Typical mature pileus (Pls. IV; V, Fig. 2) small, often reflexed, mostly less than 3 cm. broad; usually on Prunus in America, but known on other rosaceous hosts.

Fomes pomaceus and *Poria laevigata* are two polypores of this brown group that grow relatively rapidly in culture at 25°C . In culture *F. pomaceus* produces a thin mat that does not peel readily from the agar, whereas the mat of *P. laevigata* is tough and separates easily from the agar (2). A wintergreen odor is distinctive in *P. laevigata*.

Fomes pomaceus differs in its reaction on gallic acid and tannic acid media from *Poria laevigata prunicola*. *F. pomaceus* belongs to group 5,² in which there is no growth or only a trace on gallic acid medium, and on tannic acid a mat of only 25 mm. or less is evident after seven days. In *P. laevigata prunicola* the mat diameters are about equal on both media in a similar period.

Fomes pomaceus Crataegii (Pers.) Baxter³ (on Crataegus)

Typical mature pileus (Pl. III) resupinate with conspicuous gray margins. Growing on Crataegus.

Poria laevigata (Fr.) Cooke⁴ (on hardwoods, especially birch)

Mature fruiting body (Pl. VI, Fig. 1) resupinate and usually growing on birch and often covering 30 cm. or more of the surface of the

² Classification of Davidson, Campbell, and Blaisdell (5).

³ Complete description presented in Paper V of this series, "Some Resupinate Polypores from the Region of the Great Lakes," *Pap. Mich. Acad. Sci., Arts, and Letters*, 19 (1933): 305-332.

⁴ Complete description presented under the name *Fomes igniarius laevigatus* in Paper V of this series (1). Cultures of *P. laevigata*, regardless of their source or type of substratum, show little or no growth at 35°C . In Paper XVI the plant there tentatively named *Fomitiporella floridana* (?) Race I is now identified as *P. laevigata* on Carpinus by means of reactions in culture.

wood. This plant differs from both *Fomes igniarius* and *F. igniarius nigricans* in being resupinate and in having smaller pore mouths. Setae are present in all these plants, but they are infrequent in *Poria laevigata*. This character, however, is only a relative one.

Features observed in cultures will readily separate *Poria laevigata* from *Fomes igniarius* and *F. igniarius nigricans*, and likewise from the species *P. spiculosa* and the form of *P. laevigata*, designated here as *P. laevigata prunicola*. *P. laevigata* (Pl. X) develops more rapidly (41 mm. in two weeks) at 25° and 30° C. than does *F. igniarius nigricans* (24 and 36 mm., respectively, in two weeks), and also produces a denser and lumpier type of mat. *P. laevigata prunicola* grows still more slowly (5 mm. at 30° C.) than *P. laevigata*, and *P. spiculosa* differs from all three in being the only one of the group that grows rapidly at 35° C. (nearly filling the petri dish). Cultures of *P. laevigata* produce a distinct wintergreen odor at 30° C. in 14 days (1, No. XVI; 9; 11).

Poria laevigata forma **prunicola** (Murr.) comb. nov.⁵ (on Prunus)

Mature fruiting body (Pl. VII, Fig. 1) resupinate, often becoming widely effused up to 3 meters. Species of Prunus, rather than of Betula (as in *Poria laevigata*), are common substrata. Morphologically *P. laevigata* and the form on Prunus are similar, but they differ in culture. Setae are infrequent in both *P. laevigata* and *P. laevigata prunicola*, but are usually shorter in the form than in the species *P. laevigata*. *P. laevigata prunicola* produces a red mottled rot in species of Prunus, but no cankers or sterile mycelium appear. Canker formation may result if standing trees are attacked by *P. laevigata*.

In culture the two fungi differ considerably. *Poria laevigata prunicola* (Pl. X) is much lighter in color than *P. laevigata*, and it grows more slowly, especially at 30° and 35° C. In two-week-old cultures *P. laevigata prunicola* grows only 5 mm., with little or no development at 35° C.

Poria laevigata prunicola cultured in gallic and tannic acid media (2) produces a mat of about equal diameters on both media in a seven-day period, whereas in *Fomes pomaceus* there is no growth or only a trace on gallic acid medium, and on tannic acid medium a mat of only 25 mm. or less is evident in a similar period.

⁵ Complete description presented under the name *Poria prunicola* in Paper V of this series (1).

Poria spiculosa Camp. & Davidson differs morphologically from *Poria laevigata prunicola* in its abundant setae. It grows mostly on hickory and, like *P. laevigata*, produces cankers and a sterile mycelium on standing trees.

Poria spiculosa Camp. & David. (on hickory)

Mature fruiting body (Pl. VI, Fig. 2) resupinate, becoming effused up to 1.5 meters on thoroughly decayed logs of hickory and oak, usually associated with trunk cankers or unhealed branch scars. Setae are abundant. For complete description see reference 3 in the literature cited.

In cultures *Poria spiculosa* does not produce a wintergreen odor (characteristic of *P. laevigata*), and the mat formed is tough and leathery. *P. spiculosa* (Pl. X) grows equally well at 25°, 30°, and 35° C., whereas *Fomes igniarius nigricans*, *P. laevigata*, and *P. laevigata prunicola* exhibit little or no growth at 35° C. *P. spiculosa* has much greater development at 30° and 35° C. in two weeks, and grows into a more leathery type of mat than does *P. punctata*.

Although it is convenient to use the kind of wood or substratum on which the fungus is growing as a means for giving these plants a temporary designation in the field (usually birch and maple for *Poria laevigata*, Prunus for *P. laevigata prunicola*, and Carya for *P. spiculosa*), cultures are necessary for critical studies.

Poria punctata (Fr.) Cooke⁶ (mostly on alder, sumac, locust, and willow)

Mature fruiting body (Pl. VII, Fig. 3) resupinate, adnate, never loosening from the substratum, often cracking on drying; on willow, poison sumac, locust, and a large variety of hardwoods. Fruiting bodies are characterized by usually being several times laminated and forming a well-defined, more or less orbicular sporophore, i.e. not widely effused in broad plates over the substratum. This fungus is widely distributed over North America, but occurs more abundantly north of the Gulf States.

In culture *Poria punctata*, unlike *P. laevigata*, *P. spiculosa*, and *Fomitiporia dryophila* (a southern plant), exhibits little or no growth at 30° and 35° C., and the mat is more cottony in texture. It differs

⁶ Complete description presented in Paper VII of this series (1).

further from *P. laevigata* in that no wintergreen odor is produced. Cultures of *P. punctata* (Pl. X) and *P. laevigata prunicola* are generally similar in rate of growth and in their temperature for optimum development (25° C.), but *P. punctata* forms a mat much more cottony in texture.

Fomitiporia dryophila Murr.⁷ (mostly on northern live oak)

Mature fruiting body (Pl. VIII, Figs. 1, 2) largely resupinate but usually becoming somewhat ungulate and suggesting the form of an abortive Fomes, as in *Fomes robustus*, for example; *F. dryophila* is effused-reflexed in most collections. The fungus is southern in its distribution, occurring on live oak and the southern gum trees. It is usual for the fruiting bodies of *F. dryophila* to occur on dead limbs of standing trees or on trunks of living trees. (Most resupinate polypores of the genus *Poria* occur on fallen timber.)

Fomitiporia dryophila has more of a tendency to become ungulate (Pl. VIII, Fig. 2), a feature that distinguishes it from *Poria punctata* and *P. floridana*. Field collectors will recognize at once that *Poria punctata*, *Fomitiporia dryophila*, and *Fomes robustus* constitute a group of closely related plants that may be arranged in order of their general appearance. Furthermore, these fungi may be arranged by their more or less geographical occurrences or they may be grouped, when broadly interpreted, with reference to their substrata or hosts. A classification based upon habit of growth, geographical occurrence, and substrata or host relationships would result in the following order: *Poria punctata* (a resupinate that is widely distributed from Alaska and the Northwest Territories eastward to Newfoundland and southward through at least eight Canadian provinces and twenty-nine states, including Mississippi, Florida, and Texas; found on sixty-one different species of wood); *Fomitiporia dryophila* (mostly a semi-resupinate plant which is chiefly known from the states that border the Gulf of Mexico; usually growing on oak, mostly on laurel and live oak); and *Fomes robustus* (sometimes semiresupinate, but more often large, ungulate; characteristically occurring on oak, but known on other woods in Europe, including even the conifers if *F. Hartigii* is considered synonymous [see page 105]). A number of American

⁷ Complete description presented in Paper VIII of this series (1). Also see *Fomitiporia Earleae* in the same volume. This species is synonymous with *F. dryophila* and is included in this paper as Forms II and III of *F. dryophila*.

specimens are referred to *F. robustus*. The majority of these, however, are neither as large nor as rimose as the typical European plants. In rimosity it is similar to old North American specimens of *F. Everhartii*.

In culture, *Fomitiporia dryophila* differs from *Poria punctata* in having a definitely less cottony mycelial mat (see Pl. X for mat of *P. punctata* designated as being cottony) and from both *P. punctata* and *Fomes robustus* in having a faster rate of growth at 30° C. Likewise, *F. robustus* is intermediate in its growth rate between the relatively fast *Fomit. dryophila* and the relatively slow *P. punctata*. *P. punctata* has a more cottony mat than the other two fungi. There is no marked difference in color between the isolates of *P. punctata*, *Fomit. dryophila*, and *F. robustus*.

Cultures of *Fomitiporia dryophila* (Pl. XI) grow much more at 30° C., and even at 35° C., and are usually darker, than those of *Poria punctata*. *F. dryophila* produces more growth at 35° C., and the mat is more cottony than that of *Fomes robustus*. Cultures of *P. floridana* nearly fill the petri dishes at 35° C. (in two weeks), whereas those of *F. dryophila* do not.

Poria floridana (Murr.) Sacc. and Trott.⁸ (on southern woods)

Mature fruiting body (Pl. XII, Figs. 1, 2) resupinate, effused up to 45 cm., the pore surface exhibiting a sheen (velvety appearance and refracting light [glistening] much as does that of *Fomes Everhartii*). This feature is not striking in specimens of *Fomitiporia dryophila*. *Poria floridana* grows on logs of oak, red gum, and *Carpinus*, and, like *F. dryophila*, is apparently more common in the South. The tubes are whitish-stuffed in *P. floridana*, rather than yellowish-stuffed, as described for *F. dryophila*.

This species strongly resembles *Poria melleopora* (Murr.) Sacc. and Trott. It differs in not having pale brown spores, as does *P. melleopora*, and Lowe (9) adds that the hyphae of the subiculum are smaller.

Poria floridana, like *P. spiculosa*, grows almost equally well at 25°, 30°, and 35° C. (27, 28, 21 mm., respectively, in two weeks), but the mat is more cottony in appearance and does not fill the dish as rapidly as does *P. spiculosa* (which grows about 41 mm. in two

⁸ Complete description presented in Paper IX of this series under the name *Fomitiporella floridana* Murr. (1).

weeks). *P. floridana* (Pl. XIII)) grows more rapidly at 35° C. in two weeks than does either *Fomitiporia dryophila* or *Fomes robustus*.

Fomes robustus Karst.⁹ (on oak, other hardwoods, and conifers)

Mature fruiting body (Pls. XIV; XV, Fig. 1) ungulate to appimate, up to 15 cm. broad, smooth, on birch and oak (and other hosts, including conifers, at least in Europe). *Fomes robustus* differs from *F. igniarius* in that its tubes are not whitish-stuffed, but are golden brown.

Cultures of *Fomes robustus* (Pl. XVII) may be distinguished from those of *Poria laevigata* by the rate of development at 25° C. (*F. robustus*, 24 mm.; *P. laevigata*, 41 mm. for two weeks) and by the mat formation, which is more cottony than that of *P. laevigata*. (Growth of *F. robustus* cultures may be variable at 30° C.) *F. robustus* differs from *P. spiculosa* at 35° C. because it shows little or no growth, whereas *P. spiculosa* nearly fills the petri dish at that temperature.

Fomes robustus develops more rapidly and with more luxuriant mycelium than does *F. robustus Tsugina* (6, 7, and 0 mm. at 25°, 30°, and 35° C. for two weeks). It differs in rate of growth from *Poria floridana* and *Fomitiporia dryophila*, both of which produce a larger mycelial mat at 35° C. in two weeks. The rate of development at 30° C. (20 to 41 mm.) will serve as a means by which it may be separated from *P. laevigata prunicola* (3 to 5 mm.).

Fomes robustus Karst. *Tsugina* Overh.¹⁰ (on hemlock)

Mature fruiting body (Pl. XV, Fig. 2) resupinate, becoming broadly effused, usually on hemlock. Mouths are whitish-stuffed, whereas those of *Fomitiporia dryophila* are ferruginous. This fungus becomes much more effused over the substratum than does *Poria punctata*.

Cultures of *Fomes robustus Tsugina* (Pls. XVII; XVIII) do not develop as fast at 25° and 30° C. (5 and 7 mm., respectively) as do those of *F. robustus* (which grows at least 20 mm.). Since *F. robustus Tsugina* does not produce mycelial growth at 35° C., it may be separated from other fungi that do (*Fomitiporia dryophila*, *Poria floridana*, *P. punctata*, *P. laevigata*, and *P. spiculosa*). Neither *F. igniarius nigricans* nor *P. laevigata prunicola* exhibits growth at 35° C., but

⁹ Complete description presented in this paper, page 108.

¹⁰ Complete description presented under the name *Poria tsugina* in Paper V of this series (1).

both have much more luxuriant mycelial formation at 25° C. than does *F. robustus Tsugina*.

Fomes robustus Abietis forma nov. (on the true fir)

Mature fruiting body resupinate, resembling *Fomes robustus Tsugina*, but found on species of *Abies*.

Cultures of *Fomes robustus Abietis* (Pl. XVIII) may be distinguished from all other fungi in this group by the unusual growth pattern, viz., 1, 15, and 0 mm. at the end of two weeks at 25°, 30° and 35° C.

Fomes robustus forma **juniperinus** comb. nov. (on juniper)

Morphologically *Fomes robustus juniperinus* (*Fuscoporia juniperina* Murr.) resembles *F. robustus* forma *Taxodii* (Pl. XVI, Figs. 1, 2). The two are considered identical species in this paper, but the form names are retained. On the basis of present knowledge of *F. robustus* it appears that races do exist. It is known that cultures of isolates from hemlock (both *Tsuga canadensis* and *T. heterophylla*) in many widely separated regions differ from cultures obtained from the fir isolate (*Abies concolor*) in both rate of growth and mycelial features.

The forma "*Taxodii*" occurs so much more commonly than the one on juniper that it appears that two possible forms or races, "*juniperinus*" and "*Taxodii*," may exist. At least they are kept separate until evidence shows them physiologically alike in their responses. If it is determined later that the reactions are similar in culture, the name "*juniperinus*" will be recognized, since it was established earlier than "*Taxodii*."

Fomes robustus forma *Taxodii* Baxter¹¹ (on bald cypress)

See discussion under *Fomes robustus juniperinus*.

Fomes robustus Karst., Finl. Bas. in Bidr.

Finl. Nat. o. Folk., 48: 467. 1889

Plate XIV

Fomes ignarius var. *Pinuum* Bres., Rev. Myc., 12 (47): 105. 1890.

Fomes Bakeri (Murr.) Neuman, Bull. Wis. Geol. and Nat. Hist. Surv., 33: 168, t. 6, f. 27a, p. 170; t. 7, f. 27b-d. 1914.

¹¹ Complete description presented in Paper XVIII of this series (1).

- Fomes igniarius Abietinus* ex Lloyd in Synopsis of the Genus Fomes, p. 243. Cincinnati, 1915.
- Fomes setulosus* Lloyd. Syn. Fomes, p. 243. (ex Lloyd). 1915.
- Fomes robustus* var. *Pinum* Bres. Icon. Myc., Tabula 993. 1931.
- Fomes aestriplex* Ernst. H. L. Krause, Basidiomycetum Rostochiensium, Supplementum Tertium, No. 404 (according to exsiccati.). Teste Kavina et Pilát, Atlas des Champignons de l'Europe. 1936.
- Ochroporus robustus* (Karst.) Schroet. ex Donk in Rev. der Niederländischen Homobasidiomycetae, No. 9: 248. 1933.
- Phellinus robustus* (Karst.) Bourd. et Galz. in Bull. Soc. Myc. Fr., 41: 188. 1925.
- Phellinus robustus* var. *Hartigii* (All. & Sch.) in Bourdot et Galzin, pro parte, Hymen. de Fr. 617. 1928.
- Placodes roburaneus* Quélet, Fl. Myc., 400. 1888 (non Fries). Teste Kavina et Pilát, Atlas des Champignons de l'Europe. 1936.
- Placodes Hartigii* (All. & Sch.) Huber in Ztschr. f. Pflanzen., p. 4. 1927.
- Polyporus Hartigii* All. & Sch., Fungi Bav. ex Cent. 1, No. 48. 1890.
- Pyropolyporus Bakeri* Murr. North Am. Fl., 9: 104. 1908. Teste Kavina et Pilát, Atlas des Champignons de l'Europe. 1936.
- Pyropolyporus Robinsoniae* Murr. (ex Bres.). North Am. Fl., 9: 108. 1908.

Fructification sessile, woody, compressed-ungulate to appanate, 3–9 × 3–15 × 2–4 cm.; surface smooth, at least scarcely rimose, two or three times deeply sulcate, at first “snuff brown,” “wood brown” becoming gray or black, i.e. “drab,” “hair brown” to black; margin thick, broad, rounded, smooth; context zonate, glistening brown, “clay color,” 0.5–2 cm. thick; tubes stratified, more or less whitish-stuffed in the older layers, 1–5 mm. long each season; mouths mostly 5–6 to a mm., edges entire; basidia 10–15 × 7–10 μ ; spores smooth, hyaline, globose, 5–7 μ ; setae none; hyphae seldom branched, brown, 2.5–5 μ in diameter.

Forms.—*Fomes robustus Tsugina* Overh. (= *Fomitiporia tsugina* Murr. North Am. Fl., 9: 9. 1907. *Poria tsugina* (Murr.) Sacc. and Trott. in Sacc., Syll. Fung., 21: 332. 1912.)

Fomes robustus Abietis forma nov. (= *Fomes robustus Tsugina* on *Abies concolor*).

Fomes robustus juniperinus forma nov. (= *Fuscoporia juniperina* Murr. North Am. Fl., 9: 4–5. 1907).

Fomes robustus Taxodii Baxter (Pap. Mich. Acad. Sci., Arts, and Letters, 37: 193–194. 1946).

Allied species.—*Fomes robustus* is likely to be mistaken for *F. Everhartii*. The presence of the conspicuous setae in *F. Everhartii* will enable one to distinguish between the two fungi. In North

America the resupinate or semiresupinate form *Tsugina* is generally similar except in habit of growth. My experience with *F. robustus* in Europe has been with the species on oak, but it is reported on pine, spruce, and fir from that continent. Lloyd (7) holds that, notwithstanding the vastly different host for *Fomes Hartigii* (the silver fir, *Abies pectinata*), *F. Hartigii* and *F. robustus* appear to be the same in all characters. On the other hand, Lohwag (8) believes that the fungus on conifers in Europe is *F. Hartigii*. He states that *F. robustus* occurs exclusively on oaks and chestnuts, whereas *F. Hartigii* grows only on coniferous wood. Lohwag reports that *F. robustus* in time develops some fissures on the surface of the fruiting body and that these are seldom present in *F. Hartigii*. He finds that the fruiting bodies of *F. Hartigii* are generally smaller than those of *F. robustus*. Characteristic of the fruiting bodies of *F. Hartigii* are the numerous pits on the surface of the pileus that are caused by drops of water. These, he states (8), are seldom observed in *F. robustus*.

It is pointed out that tube development in *Fomes Hartigii* begins relatively late, and, in contrast to *F. robustus*, the layer of tubes does not develop directly a new tube layer. Instead, rather thick layers of trama occur between the rows of tubes. A further distinction between the two plants is made with reference to the mode of attachment of the fruiting body to the tree. *F. Hartigii* is mounted with its entire base upon the substratum, whereas *F. robustus* breaks out from the wood with its younger part, and only the most recently developed part lies just outside the bark. Therefore, large fruiting bodies of *F. robustus* are to be separated from their substratum without too great difficulty—and only a small place of attachment is pulled away. *F. Hartigii*, on the other hand, can be taken off in its entirety. *F. robustus* appears to grow faster.

In North America the form *Tsugina* commonly grows in a resupinate condition on both eastern and western hemlock, but there is little morphological difference to be noted between *Fomes robustus Tsugina* and the species on oak in Europe. The form, however, is not the same physiologically, although resemblances in color and formation of wavy brown lines in cultures can often be seen. Although the lines formed in *F. robustus* are more conspicuous than those in *F. robustus Tsugina*, the chief difference

between the plants is in their varying rate of growth in culture. *F. robustus* develops about twice as fast as *F. robustus* Tsugina.

Fomes robustus and *F. rimosus* may be confused. The smoother pileus of *F. robustus* should enable one to distinguish the two plants. The spores are brown in *F. rimosus* and hyaline in *F. robustus*.

Fomes igniarius is readily distinguished from *F. robustus* by the fact that the tubes in *F. igniarius* are whitish-stuffed instead of being golden brown.

Fomes torulosus (*F. rubriporus* Quélet), referred to by Lloyd (Fomes), belongs in this general group of plants. It has been called *Fomes fuscopurpureus*, according to him, and *Fomes rubriporus* by Boudier and Quélet. He states that he has a collection on oak from Louisiana, and that the fungus is not rare about Paris, but it is not known from England. There is a collection known from Japan, and it is probable that it will prove "to be more common in the Tropics when the distribution is better known" (7). The fungus is mentioned here because of the Louisiana record of occurrence. The fructification is described as applanate, sometimes thin, an inch or less, or other specimens 3-4 inches thick. The surface is soft when young, pubescent, at length with concentric raised, soft ridges, often with an obtuse inflated edge; context light brown (ochraceous tawny); pores minute, the tissue concolorous with the context, but the mouths at first purplish, losing the color when old and becoming brown; spores hyaline, globose, 4-5 μ ; abundant setae, projecting 16-20 μ .
Habitat index.—*Betula lenta*, *B. lutea*, *B. nigra*, *B. papyrifera occidentalis*, *Eucalyptus globulus*, *Lysiloma candida*, *Populus* spp., *Quercus borealis*, *Q. marilandica*, *Q. nigra*, *Q. texana*, *Robinia* spp., *Salix* spp., *Taxus brevifolia*.

f. *Tsugina*.—*Picea sitchensis*, *Pinus* spp., *Pseudotsuga taxifolia*, *Tsuga canadensis*, *T. heterophylla*, *T. Mertensiana*.

f. *Abietis*.—*Abies balsamea*,¹² *A. concolor*, *A. lasiocarpa*,¹² *A. nobilis*.¹²

¹² Originally listed under *Fomes robustus* Tsugina. The isolates have not been tested in culture to match that from *Abies concolor*, which shows distinct reactions in culture from *F. robustus* Tsugina.

f. *juniperinus*.—*Juniperus virginiana*.¹³

f. *Taxodii*.—*Taxodium distichum*.¹³

Distribution.—British Columbia; California, District of Columbia, Georgia, Indiana, Louisiana, Maine, Maryland, Minnesota, Missouri, New Jersey, Ohio, Oregon, Pennsylvania, Texas, Virginia, Wisconsin.

f. *Tsugina*.—Alaska; British Columbia, Ontario, Quebec; California, Colorado, Connecticut, Idaho, Maine, Massachusetts, Michigan, New Hampshire, New Jersey, New Mexico, New York, North Carolina, Ohio, Oregon, Pennsylvania, Tennessee, Vermont, Wisconsin, Washington.

f. *Abietis*.—Colorado.

f. *juniperinus*.—Arkansas, Louisiana.

f. *Taxodii*.—Georgia.

Occurrence.—*Fomes robustus* is fairly common in Europe on oak. Lloyd (7) reports it from Australia, Hawaii, and Japan.

f. *Tsugina*.—Common in regions where hemlock grows.

Cultures.—Isolated from *Betula nigra*, Great Falls, Virginia. One-year-old wood-block cultures of *Fomes robustus* mask both red-gum and white-pine test pieces with such a luxuriant growth of mycelium that the shape of the wood blocks is concealed. In luxuriant growth, color, and black line formation, cultures chiefly resemble those of *F. Everhartii*, but, unlike that species, plugs of mycelium are not formed by *F. robustus*.

Wood block cultures of *Fomes robustus* also resemble those of *Poria punctata*, and they suggest somewhat those of *Fomes nigro-limitatus*, *P. laevigata prunicola*, *P. spiculosa*, *Polyporus texanus*, *P. floridana* Race III on *Carpinus*, *Fomitiporia dryophila* Race II on *Nyssa biflora*, *Poria laevigata* on *Carpinus*, and the forma *F. robustus Tsugina*. Petri-dish tests made at different temperatures may be used, together with texture features, to distinguish *F. robustus* from *P. punctata*. See page 109.

Decay.—A yellow trunk rot is produced, which, according to Cartwright and Findlay (4), is mainly confined to the sapwood, but extends into the heartwood. The rotted part is usually surrounded by a narrow dark-brown zone of incipient decay. The

¹³ See comments in text, p. 108.

TABLE II
MYCELIAL GROWTH CHARACTERISTICS OF FOMES ROBUSTUS AND SPECIES THAT
RESEMBLE THIS FUNGUS MOST CLOSELY IN CULTURE*

Name	Rate of growth in mm. of 14-day-old petri-dish tests			Features in one-year-old wood-block tests.
	Centrigrade			
	25°	30°	35°	
<i>F. robustus</i> <i>Betula nigra</i> Virginia	24	33	1	In luxuriance of color and mycelial growth this fungus resembles <i>F. Everhartii</i> most closely. No mycelial plug forms in flasks with cotton stoppers. Best distinguishing features are exhibited in petri-dish temperature series.
<i>F. robustus</i> <i>Quercus</i> sp. Sweden	22	15	1	
<i>F. robustus</i> <i>Tsugina</i> <i>Tsuga heterophylla</i> British Columbia	6	7	0	Isolates from both <i>Tsuga canadensis</i> and <i>T. heterophylla</i> are generally similar in appearance. The form differs from the species in rate of growth as well as in being much less luxuriant in mycelial production.
<i>F. robustus</i> <i>Tsugina</i> <i>Tsuga canadensis</i> Michigan	4	8	0	
<i>F. robustus</i> <i>Abietis</i> <i>Abies concolor</i> Colorado	1	15	0	Differs from isolates of <i>Tsugina</i> in its unusual rate of growth. Intermediate between the species and <i>f. Tsugina</i> in luxuriance of mycelium, but otherwise similar.
<i>F. nigrolimitatus</i> <i>Tsuga heterophylla</i> Alaska	0	0	0	Differs from other members of the group in its exceedingly slow growth.
<i>F. Everhartii</i> <i>Quercus imbricaria</i> Michigan	24	35	5	Mycelial plugs formed in flask cultures with cotton stoppers. These do not appear with <i>F. robustus</i> .
<i>F. Everhartii</i> <i>Quercus</i> sp. Oklahoma	28	33	4	The description is like that given for <i>F. robustus</i> on <i>Betula nigra</i> .

TABLE II (Concluded)*

Name	Rate of growth in mm. of 14-day-old petri-dish tests			Features in one-year-old wood-block tests.
	Centigrade			
	25°	30°	35°	
<i>Poria punctata</i> <i>Rhus vernix</i> Michigan	24	3-10	0	Differs from <i>F. robustus</i> in its growth rate at 30° C.†
<i>P. laevigata prunicola</i> Black cherry Michigan	28	3-5	0	Rate of growth at 30° C. will sepa- rate this fungus from <i>F. robustus</i> .†
<i>Poria spiculosa</i> Hickory Pennsylvania	41	41	37	Differs from <i>F. robustus</i> in growth rate at 25° C.†
<i>Poria floridana</i> Strain III <i>Carpinus sp.</i> Louisiana	41	41	41	Differs from <i>F. robustus</i> in growth rate at 35° C.†
<i>Fomitiporia dryophila</i> Strain II <i>Nyssa biflora</i> Florida	30	38	18	Mycelium much more whitish or whitish buff as well as "cream buff." One-year-old cultures of <i>F. robustus</i> are uniform in color.
<i>Poria laevigata</i> <i>Carpinus caroliniana</i> Virginia	41	41	1	Differs from <i>F. robustus</i> in its growth rate at 25° C.

* In the tests different cultures vary slightly in their measurements for each temperature, but the relative growth expressed remains more or less constant.

† In this group mycelial wood-block cultures are not so useful for distinguishing purposes as are petri-dish temperature tests.

area attacked is usually limited to within about a yard on each side of the fruiting bodies.

Fomes robustus, like a large number of the brown resupinate polypores, grows relatively slowly in culture, as indicated in Table

II. No clamp connections are formed. The fungus exhibits a strong reaction with tannic acid medium.

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FIG. 1



FIG. 2

FIG. 1. *Fomes igniarius* on aspen, Placitas, New Mexico (courtesy of U. S. Division of Forest Pathology)

FIG. 2. *Fomes arctostaphyli* on manzanita, Klamath Falls, Oregon

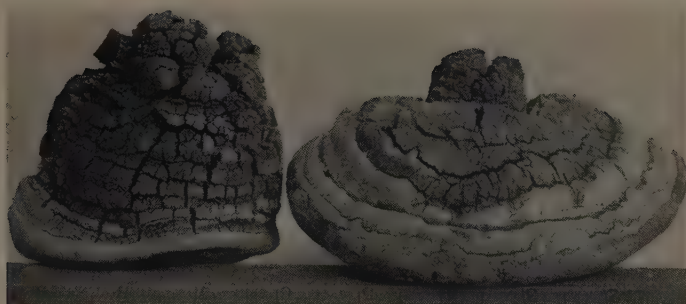


FIG. 1. Ungulate fruiting body of *Fomes igniarius* (left), Fairbanks, Alaska. Convex structure of *F. igniarius nigricans* (right) on birch, Selkirk, Yukon Territory. Mature fruiting bodies of *F. igniarius* are usually smaller than those of *F. igniarius nigricans*



FIG. 2

FIG. 3

FIG. 2. *Fomes igniarius nigricans* on *Alnus sinuata*, Valdez, Alaska

FIG. 3. *F. igniarius nigricans* growing in form similar to that of *Poria laevigata prunicola*. On yellow birch, Edmunston, New Brunswick



Fomes pomaceus Crataegii on *Crataegus* sp., Ann Arbor, Michigan. Note the characteristic margins and compare them with those of *F. pomaceus* (Pl. IV) and the "resupinate" *F. igniarius nigricans* (Pl. V, Fig. 2)

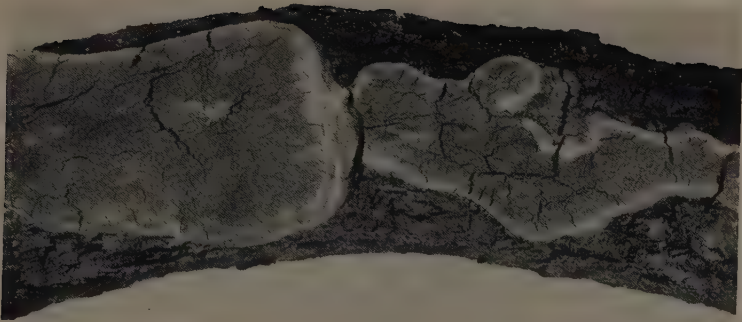


FIG. 1

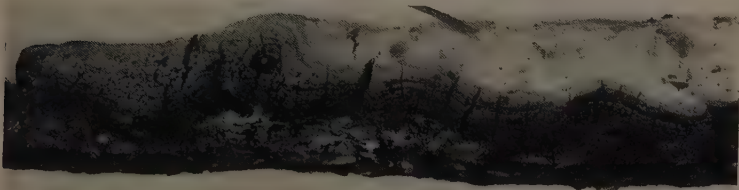


FIG. 2

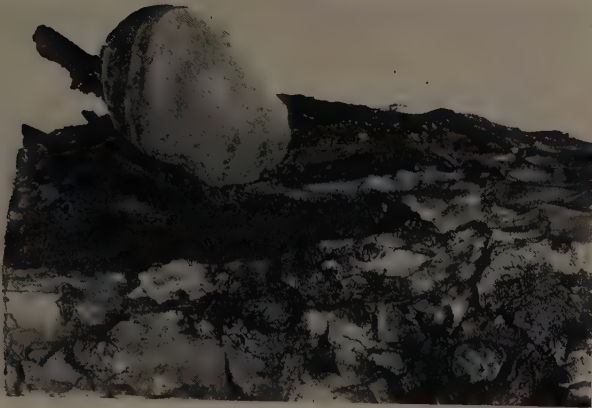


FIG. 3

Various forms of *F. pomaceus* (all specimens from Clermont Co., Ohio)

FIG. 1. Effused-reflexed form on wild plum

FIG. 2. Resupinate form on wild plum; fruiting body several years old

FIG. 3. Resupinate form on peach; fruiting body approximately one year old



FIG. 1.

FIG. 1. *Fomes igniarius nigricans* on willow, Valdez, Alaska. Note its similarity in growth appearance to *F. pomaceus* *Crataegi* (Pl. III). This growth is especially common for the species in the North.

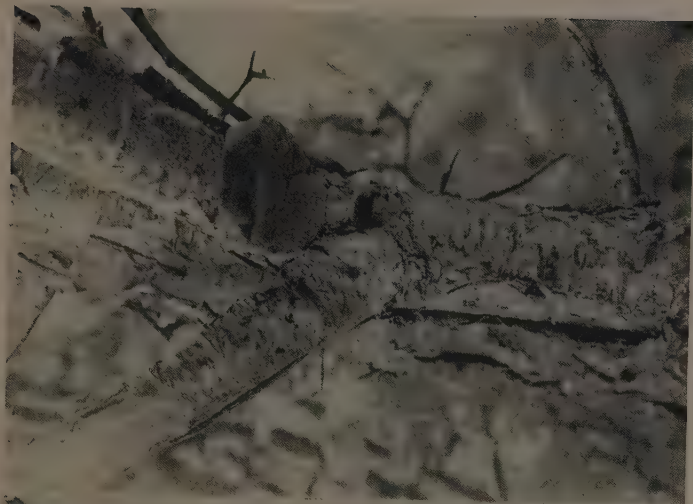


FIG. 2.

FIG. 2. *F. pomaceus*, Dismal River, Nebraska National Forest, Halsey, Nebraska



FIG. 1. *Poria laevigata* on upright yellow birch trunk, Chelsea, Michigan



FIG. 2. *Poria spiculosa* on Hickory, Crossett, Arkansas

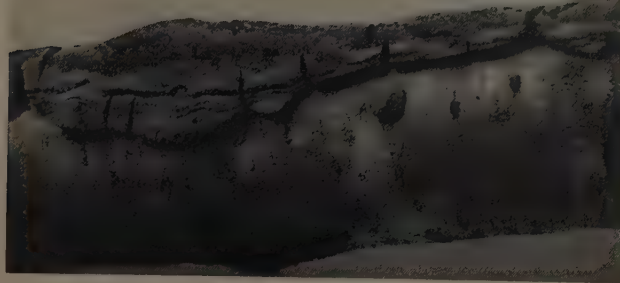


FIG. 1

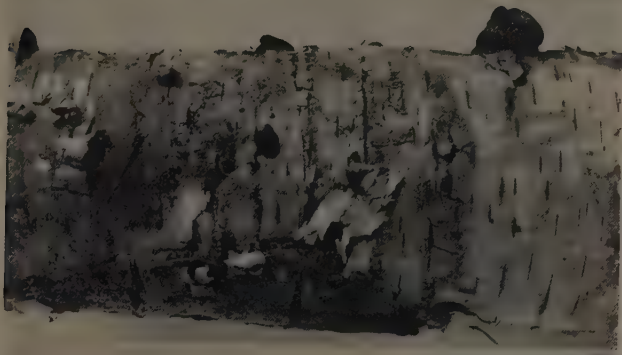


FIG. 2

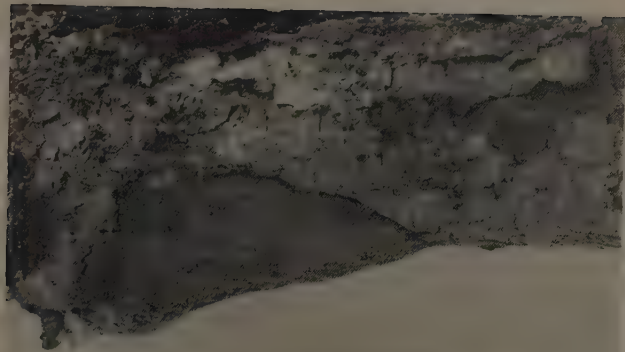


FIG. 3

FIG. 1. *Poria laevigata prunicola* on *Pinus* sp., Gander Lake, Newfoundland
 FIG. 2. *Poria laevigata* (left side) and *Fomes ignarius nigricans* (right side)
 on same log, St. Demase, L'Islet Co., Province of Quebec
 FIG. 3. *Poria punctata* on alder, Gander Lake, Newfoundland

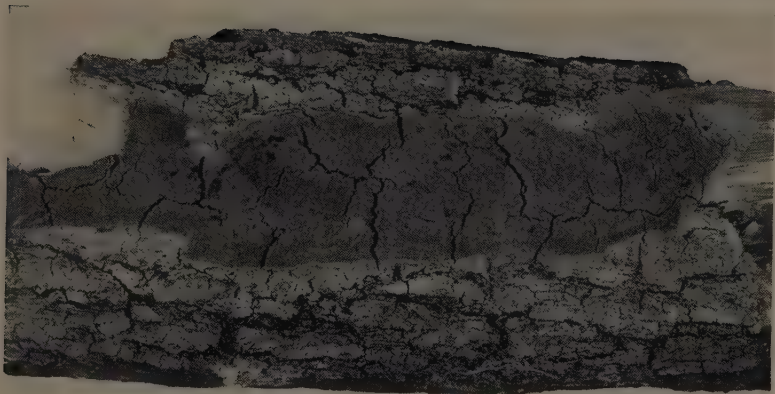


FIG. 1

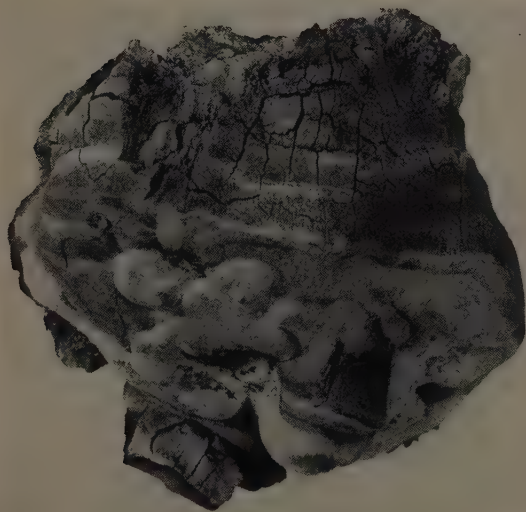
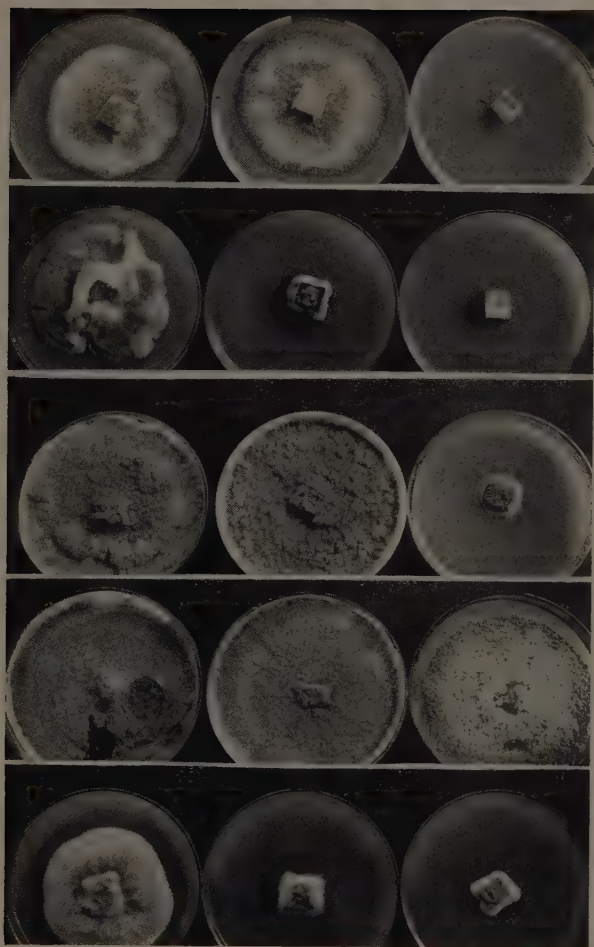


FIG. 2

FIGS. 1-2. Resupinate and effused-reflexed fruiting bodies of *Fomitoporia dryophila* on *Quercus virginiana*, Logtown, Mississippi



Poria flavomarginata on *Salix* sp., Everglades, Florida. This plant is readily distinguished by its greenish-yellow mycelium in culture



Cultures of *Fomes* and *Poria* kept at 25°, 30°, and 35° C. for fourteen days; listed in order from top to bottom:

Fomes igniarius nigricans X on *Betula kenaica*, Moose Pass, Alaska

Poria laevigata prunicola on *Prunus serotina*, Grand Island, Michigan

P. laevigata on maple, Munising, Michigan

P. spiculosa on *Carya* sp., Saltsburg, Pennsylvania; U. S. Division of Forest Pathology

P. punctata on *Rhus vernix*, Ann Arbor, Michigan



Cultures of *Fomitiporia dryophila* kept at 25°, 30°, and 35° C. for fourteen days; listed in order from top to bottom: Form I on *Quercus* sp., Ocala National Forest, Florida; Form II on *Nyssa biflora*, Osceola National Forest, Florida; Form III on *Liquidambar styraciflua*, Kingsland, Georgia

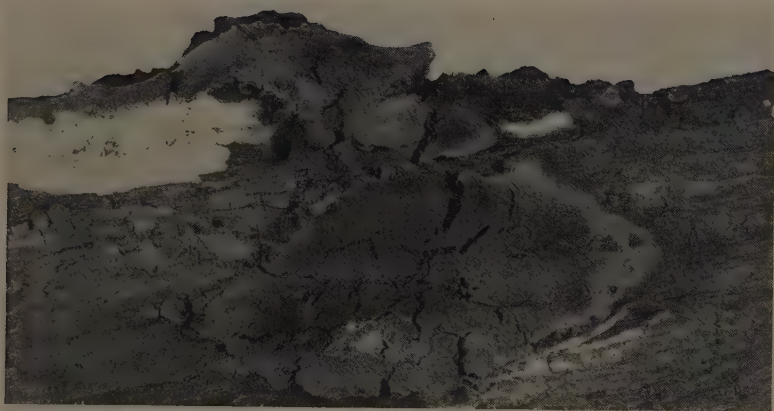


FIG. 1. *Poria floridana*, Form I on *Quercus nigra*, Waterboro, South Carolina

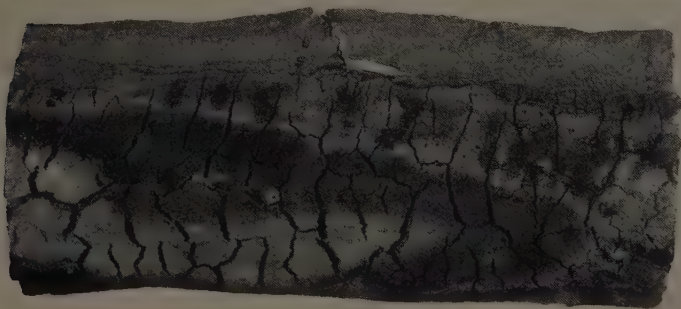
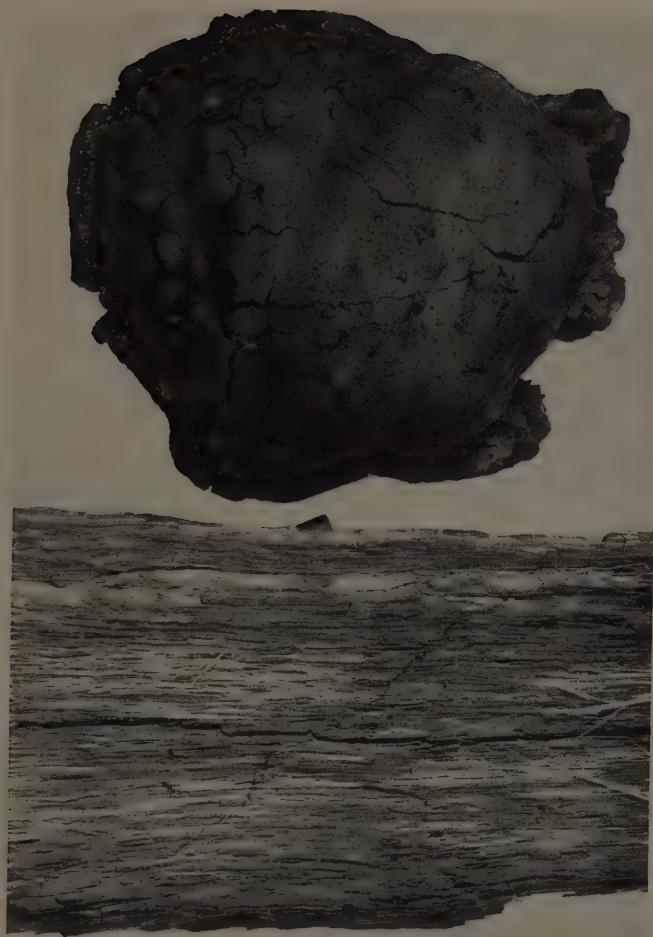


FIG. 2. *P. floridana*, Form III on *Carpinus*, Franklinton, Louisiana



Cultures of *Poria floridana* kept at 25°, 30°, and 35° C. for fourteen days; listed in order from top to bottom: Form I on *Quercus nigra*, Waterboro, South Carolina; Form II on *Quercus phellos*, Little Rock, Arkansas; Form III on *Carpinus sp.*, Franklinton, Louisiana



Decayed oak wood and fruiting body of *Fomes robustus*, Stockholm, Sweden

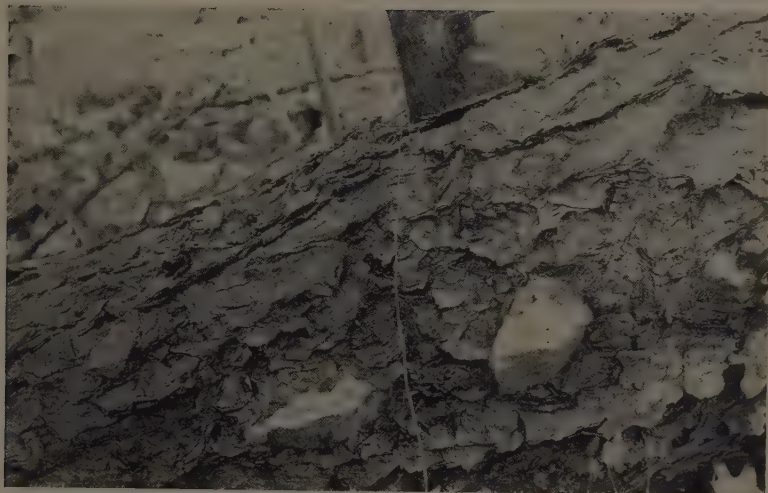


FIG. 1. *Fomes robustus* on *Betula nigra*, Great Falls, Virginia



FIG. 2. *F. robustus* *Tsugina* on *Tsuga canadensis*, Wisconsin Dells, Wisconsin



FIG. 1. *Fomes robustus* Tazodii on *Taxodium distichum*, Okefinokee Swamp, Georgia

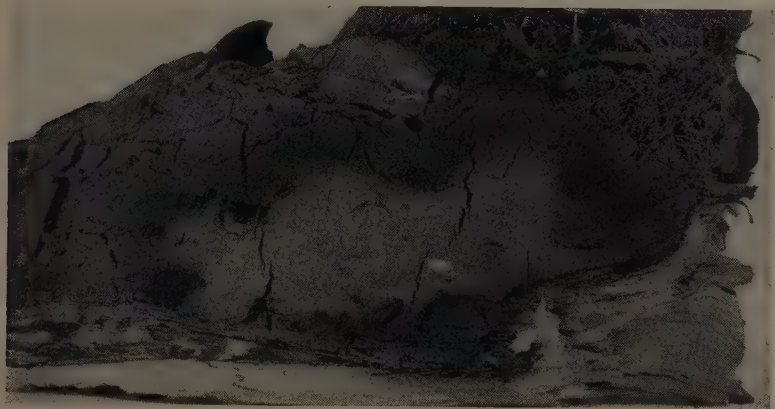
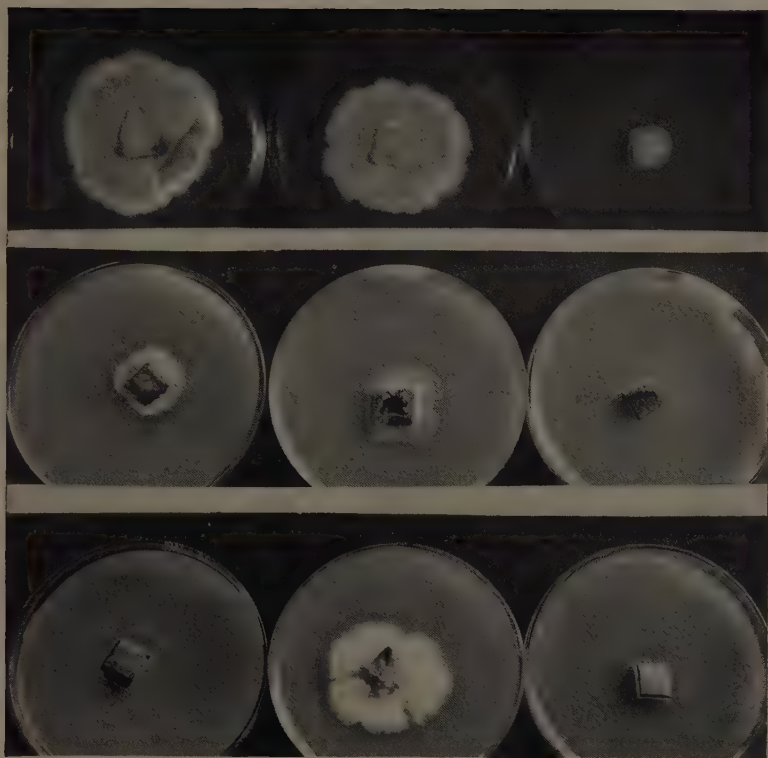


FIG. 2. *Fomes robustus* Tazodii on *Taxodium distichum*, locality unknown, Arkansas (formerly designated *Fuscoporia juniverina* Murr.; discussed in Paper XII of this series, 1)



Cultures of *Fomes* kept at 25°, 30°, and 35° C. for fourteen days; listed in order from top to bottom: *Fomes robustus* on *Betula nigra*, Great Falls, Virginia; *Fomes robustus*, culture from Stockholm, Sweden; *Fomes robustus* *Tsugina* on *Tsuga canadensis*, Marquette National Forest, Michigan



Cultures of *Fomes* kept at 25°, 30°, and 35° C. for fourteen days; listed in order from top to bottom:

F. robustus *Tsugina* on *Tsuga canadensis*, Norfolk, Connecticut; culture supplied by J. S. Boyce

F. robustus *Tsugina* on *Tsuga heterophylla*, Vancouver, British Columbia

F. robustus *Abietis* on *Abies concolor*, Sangre de Cristo Range, Colorado

THE FOREST INDUSTRY'S COÖPERATIVE RESEARCH PROGRAM

BRUCE G. BUELL

THE wood-using industries of the Lake States are definitely past the stage at which they can look to new sources of timber to keep them supplied with their annual needs. The original reserve of virgin timber is rapidly vanishing. Owners who have big investments in wood-using plants and equipment have of late years become increasingly aware of this situation. It is a plain economic fact that, as long as there is a plentiful supply of any commodity at hand, people will not (under keen competition cannot) incur expenses to replenish or safeguard that supply. I find that the majority of owners do not have the advantage of the long-term viewpoint which is drilled into us as foresters. Therefore many of them have not been as foresighted as they should be, but now, with clear evidence before them that this unlimited reserve of timber is vanishing, most owners are thinking in terms of growing timber—some, of growing it on their own lands, others, of letting someone else grow it, but all have the growth factor uppermost in their minds.

Twenty years ago industrial forestry in the Lake States was practically nonexistent; probably not over 100,000 acres of industry-owned forests were under management. It has been only during the past ten years that industrial forests have been developed to the point where they have become a major factor in our overall scheme of forest management. Today a quick survey of the eleven pulp and paper mills mentioned later in this paper indicates an ownership of 1.5 million acres. In addition, there are other pulp and paper mills, sawmills, mining companies, and many smaller owners not included in this survey, so that it seems safe to say that there are 3 to 4 million acres of industrial forests in the Lake States now under systematic forest management. The exact figure is not important. It is significant that the acreage is substantial and rapidly increasing.

When the management of a paper mill has to face the problem of

owning lands and growing timber crops, it considers two questions: (1) Must it do so in order to get the wood it needs? (2) How much will it cost per cord?

With regard to the first question, let us look at the landownership pattern first. The following figures are taken from a recent publication of the Forest Service—*Forest Resources of the Lake States Region* (1950), by R. N. Cunningham and the Staff of the Lake States Forest Experiment Station. We find that of 50 million acres of forest land in the Lake States 7 million are owned by the Forest Service, 8 million by the States, and 6 million by the counties—a total of 21 million. Of the remaining 29 million, 14 million are in “farm woods.” Presumably much of this acreage consists of woodlots in the southern parts of the States and is in hardwoods. In any case, the farm woodlots have the poorest management, and the lowest growth rate of all the classes of forest ownership. Also, a very high percentage of the yield of these woods is used locally, either by the owner or by his neighbors, so that for the most part they can be eliminated from the picture so far as production of pulpwood is concerned. This leaves us with only 15 million acres available for industry and private ownership of all kinds, and of this amount 3 million acres are already owned by pulp mills.

Cunningham states that we may expect a growth of about one sixth of a cord (16 cu. ft.) per acre per year for the next twenty years. He also says that only 26 per cent of the present use of forest production is in the form of pulpwood. Hence pulp mills will grow approximately 500,000 cords of wood on their own lands, of which 130,000 will be pulpwood. On the 12 million acres of private land we may expect 2,000,000 cords, of which 520,000 will be pulpwood. On the 22,000,000 acres of land in public ownership we may expect 3,700,000 cords, of which 960,000 will be pulpwood. Thus we have a total growth of 6,200,000 cords, of which 1,620,000 can be allotted to pulp mills if we assume that present-day consumption of all forest products continues unchanged in comparative percentages and in species.

The consumption of pulpwood produced in the Lake States amounts to about 1,700,000 cords. I do not want to go into this situation in detail, but I use this merely to point up the fact that our total growth will just about take care of the total drain on pulpwood, with nothing to spare unless we switch to other species, or raid the

supplies now going to other industries, or practice closer utilization. This emphasizes the necessity of doing all we can to step up growth on all lands, public and private, to meet future demands. It also shows very vividly that competition for wood will be keen; and when it is keen, the production from public lands cannot be depended on to sustain any given plant. The only way publicly owned timber can be sold is to the highest bidder. Thus a manufacturer who can make a high profit from his finished product can and will bid higher for stumpage than a competitor who has a lower profit. Market conditions change rapidly and so do profit margins. No one of sound mind would consider a big investment in a plant without assured stability of the supply of his raw material. This assurance the public agencies cannot give; therefore a certain amount of ownership by industry is a "must."

Let us take up the second point, the cost of producing wood on industry-owned land. This is a matter for a cost-conscious forester to work out. His primary consideration must be that his company needs all the wood which he can produce. If he is to be successful, he must then produce that wood at a cost that will not be out of line with what similar wood brings in the open market. What measures can he take and what expense may he incur and still accomplish this?

First of all, the forester has to evaluate the carrying costs of his land. Annual taxes and protection and administrative costs are constants, but are rising steadily as our dollar value drops. It costs just as much to carry an acre of idle land as an acre of good growing timber. He must therefore get his idle land to working. He will also have some lands which are poorly stocked, others growing species of low value, or species which are of no use to his particular industry. He will have swamps that are stagnant and stands of reproduction too thick for good growth. He is faced with problems of excessive loss through fire, disease, insect attack, windstorms, and ice and snow storms, all of which cut into the growth rate for his property. He will have other areas that do not reproduce well after cutting. His problem is to do what he can to combat all these adverse factors and still show a net profit for his operations.

During the past few years stumpage values have risen along with labor costs and everything else. This has given our management

forester opportunities to practice some silviculture that has been impossible in past years, and still keep his figures on the ledger in ink of the proper color.

But what measures is he to take, and what will give the best results per dollar spent? A few of us have been industrial foresters for twenty years, and many more for lesser periods. Upon comparing notes we find that we disagree on almost every point save one. That one is that "we don't know." These silvicultural methods are rapidly becoming of more importance to us. In our search for the answers we find that the Forest Experiment Station has done a great deal of work; the various schools and other agencies have done some. But much of it has been concerned with sawlogs, particularly hardwoods, and a large part of the information published has been based on small-scale experiments, which are necessarily limited in scope and hence lack region-wide accuracy.

During the past few years nearly every one of the major pulp and paper companies has done some practical research on its own lands. This work has varied widely, depending on the needs of the company and the individual ideas of the foresters in charge. Much of it has duplicated that done elsewhere, a large portion of it has been incomplete, and very few of the results have been made available to others. Thus the need for much more research, with a much broader base taking in more data gathered from a wider variety of locations, has become apparent.

One of the big problems that has worried many of us as landowners and as pulpwood users has been the terrific loss in our poplar stands because of the Hypoxylon canker. Very little is known about it, its prevalence, rate of spread, and, particularly, how it can be stopped. For a number of years several of us have talked to those we thought should be interested, the Forest Service, the Experiment Station, the forest schools, and the Departments of Conservation. Finally, in 1949 Dr. Ray Hansbrough, senior pathologist in charge of the New England Section of the Bureau of Plant Industry, was given the assignment of seeing what could be done. It is noteworthy that we had to go to New England for a pathologist. We have none in the Lake States attached to the Forest Service or to any of our state conservation departments. Dr. Hansbrough, being a very busy person with all of New England to cover, could spend only a month or so in the Lake States. Most of his time available for the Lake

States had to be devoted to studying the problem and getting the field procedure organized. He could do little of the field work personally. The funds allotted to him allowed him to hire one young forester as an assistant for the summer months. In order to speed up the work we at Northern Paper Mills assigned one of our foresters to help, which enabled us to get the data on twice the number of plots that would otherwise have been possible. Thus the work was started. The Government funds allocated for this work for 1950 were to be no larger than those for 1949, so that I got in touch with a few other mills, found that they were interested, and called for a meeting with Dr. Hansbrough to plan for the work in 1950. Representatives of five mills attended, and in a few moments Dr. Hansbrough was pledged all the assistance he could possibly use.

From this meeting came the suggestion that we combine and push research on other problems in the management of poplar lands. Calls for another meeting were sent out, and eleven mills responded. Again a little discussion quickly broadened the scope, this time to take in management problems of any or all other species rather than just poplar. The meeting was followed by another one with the staff of the Lake States Experiment Station. It was suggested that industry could supply the manpower to do the field work for many of these research problems; the work would be done on their own lands; industry would get the benefit of the training and increased interest of their own personnel. The Experiment Station would furnish the needed planning and correlation of the projects and publish the results.

The industry group suggested that the field was large enough to have the Station assign a full-time man to promote, organize, and correlate these industry projects. Being limited for the immediate present by their current budget, the Station was unable to do that. A program was set up for the year of 1950, however, and the following projects were planned for action: (1) continuance of the Hypoxylon canker study; (2) study of reproduction under various conditions in our spruce, balsam, and cedar swamps; and (3) discing to promote reproduction.

Early in March, 1951, another meeting was held in St. Paul to review the results of the previous year's activities. Dr. Hansbrough reported on the Hypoxylon study. A wealth of data was on hand, but only the major factors had been analyzed, owing to lack of

personnel. Much more remains to be done on the analysis alone. No definite solutions for the control of this disease were apparent, though there were noted two distinct trends in the incidence of it which may give us some leads. It was decided to continue the study by establishing permanent plots throughout the Lake States.

The companies offered to undertake the work of establishing such plots and to gather the necessary data. This is one of the projects on the program for the coming year (1951). The discing project will also be followed up and developed this year, as will the study of swamp reproduction. These projects seemed to be enough for the present.

Thus we have a good start on this research program. We have proved that a number of distinct advantages are gained by coöperative effort, such as the following:

1. The work of the Experiment Station can be enlarged and speeded up to a considerable extent. Timber-holding companies are glad to donate the time of their employees to work on any practical problem which is of interest to them. Many companies are interested in the same problem, so that this additional help can be very material.

2. By having their own men investigate these problems on their own land, companies can train them, keep them up to date, stimulate their interest. They see the results for themselves and do not have to try to dig them out of a mass of publications, which most of them are too busy to peruse.

3. Experiments will be carried on over much wider areas and scattered so as to cover a variety of conditions, and, therefore, results will be much sounder and more reliable than when based on limited areas in a limited region.

4. This expansion of research work can be done without the necessity of asking Congress for large increases in appropriations. I believe that on March 15 all of us agree that our government is spending too much, and doubtless wasting a large part of it, but on this type of research we get direct benefit from every dollar we spend, without a considerable portion of it being wasted in Washington before the balance is returned to us locally.

5. Research work already undertaken by the various forest schools, states, and their departments of conservation could and

should also be incorporated into this program so that the individual efforts may be added to the whole. Some of the work being done as individual efforts is now in duplication of that carried on by others, and much more progress can be achieved if all efforts are correlated. Parts of some of the problems undertaken would make excellent subjects of research for graduate students working for their master's or doctor's degrees.

Our experience has made it quite apparent that we do need two things:

1. A qualified pathologist stationed in the Lake States, presumably attached to the staff of the Experiment Station. We certainly have plenty of problems that require the services of such a man. I believe the Lake States Experiment Station is the only one in the whole country that does not have a pathologist on its staff.

2. Some one man who would have the responsibility of promoting this coöperative program to make it most effective. It will take considerable contact work in visiting various companies, becoming familiar with the problems they are individually interested in, ascertaining those which are common to several companies, and setting up the procedure so that the work can be done on a uniform basis and results can be analyzed. To do this personal contacts are needed. Correspondence cannot be effective.

It may be that one man can fill both of these needs; at least we feel strongly that these are jobs with high priorities. As a team with all pulling together we get results impossible to achieve by individual efforts.

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